

Annals
of the
Missouri Botanical Garden

Vol. 36

NOVEMBER, 1949

No. 4

ON SOME USES OF MAIZE IN THE SIERRA OF ANCASH

CHARLES M. RICK¹ AND EDGAR ANDERSON

In its long association with man, maize has had a complicated career. It has been used by various peoples and in various ways. One might compare its whole history to a complex fabric, its warp the multitudinous varieties of this versatile crop, its woof the myriad uses to which *Zea Mays* has been put by the peoples who have grown it. In interpreting and understanding this history and in developing the broadest use of this world asset, one can never predict which of these various strands will be most useful in unravelling some particular problem. One finds ethnological curiosities leading to modern technological progress; for example, waxy maize, developed by Asiatic aborigines (Collins, 1909), became the clever solution to wartime shortages of industrial carbohydrates (Sprague and Jenkins, 1948). In reporting these rather unusual uses of maize in the South American highlands we would not venture to predict whether their greatest significance might be to an historian, a biochemist, an archaeologist, a plant breeder, or to some imaginative industrialist.

Ancash is a small department including part of the Coast and Sierra of Peru north of Lima. It is largely drained by the Río Santa, one of the largest rivers of the western slopes of the Peruvian Andes. Throughout most of its length the Santa is flanked on the west by the Cordillera Negra and on the east by the Cordillera Blanca, the latter completely dominating the scenery of Ancash with its chain of very high peaks and their glaciers and perpetual snowfields. Excepting its upper and lower extremities, the large trough between these two ranges is known as the Callejón de Huailas (*sensu latu*). The Santa varies in elevation in this region from 3,370 m. at Recuay to 2,150 m. at Villa Sucre (Weberbauer, 1945). Sugar cane and other tropical and subtropical crops are cultivated under irrigation in the lower reaches, maize and small grains in the upper part, the latter

¹College of Agriculture, University of California, Davis; Fellow, John Simon Guggenheim Memorial Foundation, 1948-49.

crops being irrigated in the few areas in which the ground is reasonably flat and in which water is accessible. On the higher slopes, up to 4,300 m., pastures, potatoes, barley, fava beans, and other crops are grown without irrigation. Maize and other crops dependent upon rainfall are grown in the rainy season from October to May.

The Callejon de Huailas is one of the most populated valleys of the Peruvian Sierra. The great majority of the people are pure-blooded Indians or descendants of Indians. They live in the larger centers, in small outlying villages, or in solitary dwellings in the fields. Typical of the Peruvian Indians, they live according to the same primitive customs that their forbears have followed for centuries, almost without modification by contact with modern civilization. As a closely knit group, however, they differ in varying degrees from the *serranos* of other sections: they dress in their own characteristic costumes; their *quechua* language is greatly modified; and they deviate in certain uses of food plants. Much of the commerce and agriculture of the region is managed by a small group of pure whites, or nearly pure whites, whose life is influenced to a surprising extent by the Indians with whom they live. This influence is evident in their language and foods.

Part of the information for this publication was gathered by the senior writer from informants and from observations made during a stay of two weeks in January, 1949, in the Callejon de Huailas. We are deeply indebted to Señora Elola Haro de Guzmán, our chief informant, who offered generous hospitality and answered innumerable questions with utmost patience and understanding. She has always lived in the vicinity of Huaráz, capitol of the department of Ancash. From the time of her husband's early death, some 20 years ago, she has personally managed the affairs of the family farm or *chacra*, in which, like many Peruvian *chacras*, the Indian laborers live and work in what might be called a benevolent sharecropper basis. Through this experience and her many other contacts with people in the area, Señora de Guzmán has become thoroughly versed in the life of the Ancash Indians.

Maize, the most important food plant in the Sierra of Ancash, is used in a great variety of recipes. The most unusual use of maize and one which apparently is not known outside Ancash is *tocos de maíz* or fermented maize.

Tocos—The most popular maize variety for the preparation of tocos is *cusqueño blanco*, a variety typically having eight-rowed ears of enormous grains with soft floury endosperm. If *cusqueño blanco* is lacking, other white-grained varieties are used. The maize is used only in the mature state.

The fermentation or rotting process is conducted in the following fashion. The whole ears, husked, but with grains still attached, are placed in any quantity in a sack of linen (wool or cotton cannot be used presumably because they would disintegrate in the process). The sack is tied shut securely and is submerged in water in a hole that has previously been dug in an irrigation ditch where the water is flowing freely. The hole must be deep enough so that the sack and its contents are covered by at least two inches of water. Stones are placed on top in order to

prevent the sack from rising above water. Aside from the importance of keeping the sack submerged, the depth of submergence does not seem to matter. A very important part of the process is to place the stones and to arrange the surrounding ground and grass so that the cache cannot be readily detected. *Tocos* are very popular and therefore valuable items of commerce, and their loss by theft is by no means uncommon.

The maize can also be fermented in large pools of standing water, but it is considered that a product of better quality is produced in running water. Whether the water is standing or running it is essential that the maize be completely submerged in water in a hole in the ground.

Whatever changes occur, the fermentation must be anaerobic or semianaerobic. The length of time required for the process depends on the age of the maize and probably also on the temperature of the water. When recently harvested ears are used the fermentation is complete in two months, but if the ears are older and the grains harder it may be necessary to wait as long as three months. The stage of fermentation is determined by touch, the process being completed when the grains are soft, at which stage they are bloated and have a somewhat water-soaked appearance.

When the desired stage of fermentation has been reached, the pericarp is removed from the grains, which still remain on the ear, by rubbing with the fingers. It is not possible to do this before the fermentation is completed. The ears are then washed in cold running water. They are washed well, but gently, so that none of the starch is lost.

At this stage the *tocos* are ready for cooking and can be stored in a moist condition for no more than seven or eight days. If it is desirable to keep them for a longer period, they are dehydrated in the sun. The grains are shelled from the ears and are spread thinly in a place where they will receive the maximum amount of sunlight. Depending upon the light intensity, from four days to two weeks are required to complete the dehydration. If the grains are well dried they can be stored for one or two years under the generally cool household conditions of the Sierra. Fresh *tocos* are considered to make a better product than dried ones. They are marketed in both forms.

The usual cooking process consists of stewing them in an *olla*, or low earthenware pot with a mouth nearly as large as the largest diameter. The *tocos* are placed in the *olla* and enough boiling water added to cover them. Either refined cane sugar or *canchaca*, a crude brown sugar considered to be superior to refined sugar for this purpose, is added, the amount depending upon taste. Sugar is required to offset the natural acidity of the product. Sometimes herbs are added for flavoring, but the uses and purposes of these are not well understood and are said to be secrets of the Indians. The mixture is cooked for 20 or 30 minutes.

The odor of this dish, which is not the least bit dissipated by cooking, is reminiscent of vases of flowers in which the water has not been changed often enough. It is just barely possible for the uninitiated to stay in the same room when

tocos are served. They are much more agreeable to taste than to smell, according to the experience of the senior writer. They are eaten in great quantities without ill effect and are very popular both among Indians and whites of the region. They are probably no more offensive to us than our sauerkraut or highly scented cheeses would be to the Ancash Indian. It is conceivable also that certain valuable vitamins, possibly of the B complex, might be elaborated in the rotting process.

Tocos are generally eaten for lunch and dinner, but there is no great regularity, they being consumed also at other hours of the day. They are served warm like a stew, but are also very popular chilled after cooking. They are considered effective as a remedy against colds. There is no distinction as to age of the person eating *tocos* or occasion on which they are served. In the recollection of Señora de Guzmán they have retained a constant popularity in her time.

In the Sierra of Ancash possibly 20 per cent of the maize is consumed in the form of *tocos*. More extensive use is probably limited because they are more difficult to prepare than other maize foods. Yungay (2,535 m.) and Carhuas (somewhat higher elevation) in the Callejon de Huailas are the principal centers of preparation of *tocos*. From these centers they are transported to other markets in Ancash. Because they are in brisk demand, they sell rapidly whenever offered. The reasons for the development of this use in these places is not well understood. Climatic conditions can hardly be responsible for the restriction to Yungay and Carhuas because *tocos* of good quality can be prepared at Huaráz, which lies at a considerably higher elevation (3,080 m.).

We inquired extensively in both the Sierra and Coast of Peru, but found no evidence of the use, and very little evidence of the knowledge of *tocos* outside the Sierra of Ancash. Informants would nearly always indicate familiarity with *tocos* upon inquiry and upon mention that it was a fermented maize product, but further questioning would generally reveal that they were thinking of *chicha* or some other product and that they had never actually heard of *tocos*. It is impossible to state the antiquity of this use of maize. Since it is used universally by the Indians of Ancash and since it is known only by a name in the *quechua* language, it seems likely that its use antedates the colonial period.

We are indebted to Dr. Carl O. Sauer, of the Department of Geography, University of California, for calling our attention to the following quotation from the works of de Champlain, which leaves no doubt that a similar product was used by the Huron Indians:

They have another way of eating Indian corn, to prepare which they take it in the ear and put it in water under the mud, leaving it two or three months in that state until they judge that it is putrid; then they take it out and boil it with meat or fish and then eat it. They also roast it, and it is better that way than boiled, but I assure you that nothing smells so bad as this corn when it comes out of the water all covered with mud; yet the women and children take it and suck it like sugar-cane, there being nothing they like better, as they plainly show.—[Biggar, 1929, 3:129-130.]

A similar product, *tocos de papa*, is prepared from a potato variety called *anco* having rather dry white flesh. Methods of fermenting and even of drying the fermented tubers are almost identical to those used for maize.

According to Señora de Guzmán *tocos* have a medicinal value in addition to their putative value in curing colds. They are used in the following manner to cure filmy eye of the burro or horse. Dehydrated *tocos de papa* are finely ground and passed through a fine screen. The fine powder thereby obtained is blown into the infected eye through a small tube of paper.

Cancha—In the vicinity of Huaráz this name applies to parched maize, but in other parts of Peru it appears to be a general term pertaining to both parched and popcorn. Even in its restricted use to parched corn, it is by far the most popular form of prepared maize in the Callejon de Huailas. Perhaps 50 per cent of all the corn in the Sierra of Ancash is used as *cancha*. Almost any form of maize can be used for *cancha*, but *tercio pelo* or *maíz dulce*, a variety having starchy, hard, rounded grains of reddish brown color with a yellow tip, is preferred. Another variety, *pacchus*, apparently a true sweet corn, is also considered satisfactory for this use.

For the preparation of *cancha* (and probably also popcorn) the Indians of Ancash use a baked clay vessel called the *tiesto*, which is mound-shaped and slightly rounded on the bottom. It has a small opening on the side and may or may not have a handle. They are generally 20–30 cm. in diameter.

Valcárcel (1934) described and illustrated a similar vessel that was unearthed in the ruins of Sacsahuamán (department of Cuzco). This specimen or one very similar to it was seen by the senior writer on a visit to the Instituto Arqueológico

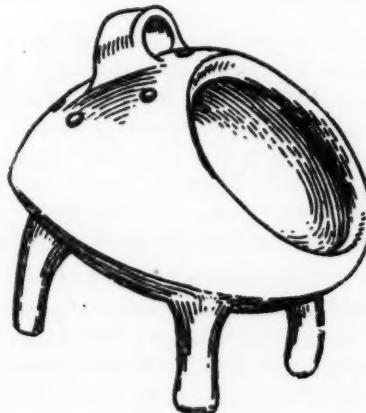


Fig. 1. *Olla canchera*, a prehistoric vessel used to parch maize. Reproduced from Valcárcel (1934).

del Cuzco and is copied by photostat from the cited paper as the accompanying fig. 1. Valcárcel describes it as follows (p. 228):

1-408—Olla canchera tripode de barro cocido. Con asa. Sin pulir y sin ornamentar. Lleva seis perforaciones cerca del asa y tiene la base ennegrecida probablemente por el fuego. Factura semifina. Por lo diminuto de su tamaño parece juguete, réplica de otros mayores. Alto 6.2 cm. Diam. de la boca 3.7 cm., Diam. de la base 6.2 cm. (Vessel of fired clay with three legs, used for preparing cancha. With handle. Without polish or ornamentation. It has six holes near the handle and its base is blackened, probably by fire. Semifine artefact. For the smallness of its size it appears to be a toy, a replica of other larger ones. Height 6.2 cm., Diameter of mouth 3.7 cm., Diameter of base 6.2 cm.)

Another example described as a brazier or small stove was illustrated by Birmingham (1930). This artefact, dug from the ruins of Machu Picchu, closely resembles the preceding one in shape, but is larger, being 17 cm. high. In his more recent book, 'Lost City of the Incas' (1948), one is illustrated opposite page 42, where it is described (erroneously, we suspect) as "A Brazier for Annealing Bronze Articles."

The *tiestos* of Ancash resemble these precolumbian *ollas* in general shape except that they have smaller mouths, lack the legs, and may or may not have the handle. The hooded form of these vessels prevents the escape of grains that jump during the parching. The senior writer has also seen *cancha* prepared in Huaráz in open earthenware vessels having the general shape of our frying pans.

To prepare *cancha* only mature grains are used. These are placed without other ingredients in a *tiesto* that is heated as hot as possible over a wood or charcoal fire. The grains are soon toasted and slightly expanded by the heat. After they have reached this stage the grains are removed and cleaned on paper or cloth. They may be flavored with melted lard and salt. A supply of *cancha* is usually not kept for more than one day. Two batches—one in the morning and another in the afternoon—are usually prepared per day.

Cancha is immensely popular in Ancash and throughout the Peruvian Andes. The parched grains may be eaten at any time of the day and at all times of the year. Everyone, children included, eat it. It is very convenient for the worker to carry a pouch of it with him at all times and to crunch away on the grains whenever hungry. When *cancha* is lacking in a household, it is bought in the market or from a neighbor. It is veritably "el pan de los indios mejor dicho." In Ancash *cancha* is not ground to prepare a flour. The only type of *arina* or flour that is prepared from maize is ground from untreated grains or from *chocchaca*.

Chiccha—This mildly alcoholic beer-like drink is by far the most important beverage of the Sierra. We are aware of several methods of preparation, but we did not investigate in detail the processes employed in Ancash since they are similar to the well-known methods of the Peruvian Sierra. Methods of preparing *chiccha* in various sections of Bolivia are described in detail by Cutler and Cárdenas (1947).

Chiccha de jora, considered the *chiccha* of best quality, is prepared from malted maize. Grains of several different yellow or red varieties are sprouted and then

dried. The grains are stored or marketed in the dried sprouted condition. These are ground and mixed with water in large earthenware jars for fermenting.

Chichas morada, another well-known product, is prepared from the maize variety known as *morada* having dark purplish grains and cobs. The dried grains are ground and the consequent flour is stewed with the cobs in water. The mixture is filtered and allowed to ferment.

Other *chichas* are prepared from barley, wheat bread, fava beans, and other crops in Ancash.

Mote—This is a form of hominy prepared from mature grains of preferably a white variety of maize. The grains are treated in a boiling lye solution (*lejia*) prepared from water and ashes, for one-half hour. The pericarp is then removed and the grains are boiled further until they burst. *Mote* is eaten in this form or is ground for the preparation of *masamoras* (puddings) or *tamales*. *Mote*, like *tocos*, can be dehydrated for storage.

Chochaca—Mature grains are shelled from the ear and cooked in a great quantity of water until they split slightly. The grains are then spread in the sun to dry and are stored for whatever time they might be needed. The drying process is facilitated by first exposing the grains to frost on a cold night before spreading them in the sun. *Chochaca* is used mostly for soups, for which purpose it is ground.

One might point up this picture of maize in these remote highlands by contrasting it with maize in the United States where it is primarily our medium for producing the maximum amount of beef and bacon per man hour per acre, and secondarily a most delicious vegetable. Or contrast either of these with uses in Mexico where it is indeed the immediate staff of life for nearly every citizen and ordinarily is eaten directly at every meal of every day in the year, as *tortillas*, *tamales*, and a variety of lesser-known foods such as *atole*, *pinole*, *posole*, etc.

It is worth noting that one of these Peruvian recipes begins by parching the kernel, another by prolonged soaking. The parching (or popping) of the kernel (usually followed by grinding it into a fine meal) is apparently one of the oldest and most widespread uses of maize. It is almost universal in the New World and is widespread in the mountains of central and southeastern Asia. Though many of the products are delicious, they have tended to disappear under the impact of modern sophistication, ultimately to reappear as the ultra-modern, ultra-sophisticated, standardized, mass-produced, trade-marked cocktail wafers such as "Fritos."

As to the prolonged soaking of the kernel, this idea seems to have its roots deep in western South America. Of a collection of recipes obtained from an old family in Antioquia, Colombia, through the kindness of Srta. Julia Guzmán Naranjo, nearly half began by soaking the kernels from overnight to four or five days or longer. It is noteworthy that recipes involving long soaking are apparently unknown to Mexican cooks or considered too trivial for polite discussion.

SUMMARY

1. The common uses of maize are described for the Sierra of Ancash, a somewhat isolated region of Peru north of Lima, with a conservative, predominantly Indian population.
2. The two commonest maize foods in the Sierra of Ancash are *tocos de maiz* and *cancha*. The former is made from kernels fermented under water for two months or longer. The latter consists of whole kernels parched in a special dome-shaped vessel called a *tiesto* or *olla canchera*. Prehistoric examples of these utensils are known from the southern highlands of Peru.
3. These foods are discussed briefly in relation to the history and geographic distribution of uses of maize.

LITERATURE CITED

Biggar, H. P. (1929). The works of Samuel de Champlain. 6 vols. Champlain Soc. Toronto.

Bingham, H. (1930). Machu Picchu, a citadel of the Incas. New Haven.

_____, (1948). Lost City of the Incas. 263 pp. New York.

Collins, G. N. (1909). A new type of Indian corn from China. U. S. Dept. Agr. Bur. Plant Ind. Bull. 161:1-30

Cutler, H. C., and Cárdenas, M. (1947). Chicha, a native South American beer. Bot. Mus. Leaf. Harvard Univ. 13:33-60.

Sprague, G. F., and Jenkins, M. T. (1948). The development of waxy corn for industrial use. Iowa State Coll. Jour. Sci. 22:205-213.

Weberbauer, A. (1945). El mundo vegetal de los andes peruanos. Min. de Agr. (Lima).

Valcárcel, L. E. (1934). Los trabajos arquelógicos del Cuzco. II. Sacsawaman redescubierto. Rev. Mus. Nac. (Lima) 3:211-234.

SPORES OF THE GENUS SELAGINELLA IN NORTH AMERICA
NORTH OF MEXICO

ALICE F. TRYON

In 1901 L. M. Underwood remarked that the old *Selaginella rupestris* was one of several examples in which segregation of species had "successively expanded to the bounds that would cause the botanists of twenty years ago to suffer acute paralysis." Among American workers Underwood had already started this segregation three years earlier. The critical studies of Van Eseltine (1918), Maxon (1918, 1920, 1921), and most recently of Weatherby (1944, 1946) have added further new species. Additional collections and critical study will no doubt bring to light still other new species. Dr. Maxon has noted the need for an examination of the species complexes *S. densa* and *S. Wallacei*.

The spores, particularly the characters of the megasporangia, have appeared to be an integral part of recent descriptions of species. Mr. Weatherby has expressed the opinion that when used cautiously the pattern of spore sculpture is useful in species definition. The present study was undertaken to present a survey and an illustrated account of the spores of our native Selaginellas.

The megasporangia are not very generously supplied with spores, each usually containing but four megaspores. Each spore has a hemispherical base and three plane triangular faces. The base or *outer face* is the free surface in the tetrad and the three plane triangular surfaces—collectively, the *commissural face*—are the sides in contact in the tetrad. The commissural face is marked by three prominent *commissural ridges* which are united at the apex and radiate out at nearly equal angles to the vicinity of the *equator*. The ends of the ridges are sometimes connected by an *equatorial ring*.

The spore surface may be smooth, granular, rugose, rugose-reticulate, or tuberculate wholly or in part. The enclosed areas in a reticulate pattern are called *areolae*. The photographs convey the type of sculpture more accurately than a descriptive statement, and, unless remarks on variations accompany the data for each species, the illustrations can be regarded as representative of the material examined.

It rarely happens that one or two of the megaspores within a sporangium may develop at the expense of the others, which are then much dwarfed. The megasporangium of *S. rupestris* usually bears two spores although occasionally three or a single spore may develop. The spores of this species characteristically lack commissural ridges but some spores bear a single straight or circular ridge. Occasionally sporangia contain one or two peculiar "dumb-bell"-shaped spores in which there has been an incomplete division (Lyon, 1905). One megasporangium of *S. pilifera* was observed to have eight megaspores.

The size of the megaspores range from 0.15 mm. in diameter in *S. armata* to 0.53 mm. in *S. selaginoides*. The measurements given in the text are of the

greatest diameter. The mode is used to express the central position of the measurements. It is printed in italic between the extremes.

The color of the spores was determined at 45 diameters, using natural light and a black background. The color range is expressed according to Ridgway's 'Color Standards.' The popular term of color approximately equivalent to that of Ridgway's is in parentheses. There is marked variation in color in some species, immature spores often being of a different shade than the mature spores.

The megasporangium was removed from the strobilus and soaked in 50 per cent alcohol. After two or three minutes it was sufficiently pliable to dissect out the spores. Some care had to be used to prevent them from escaping for they were easily blown or jarred from the dissecting field after the alcohol dried. The spores were mounted dry, on a glass or mica slide, within a ring of cement built up to support the cover glass, and this was sealed with cement.

The megaspores were photographed through a compound microscope using a 48-mm. microteliplat lens as the objective and a $15 \times$ hyperplane lens as an ocular. Additional magnification was achieved through suspending a $10 \times$ ocular above the microscope. The camera, a Bausch & Lomb Model K, with 8-inch bellows, was placed over this. An image in focus at the third lens was also in focus on the ground glass of the camera. Four Leitz microscope lamps with green filters were placed around the microscope at the level of the stage. These supplied a very satisfactory source of illumination, for the intensity and angle of the light could be adjusted for each lamp. The film used was Eastman Ortho-X, and the exposure time varied from 20 to 90 seconds.

Each microsporangium bears several hundred microspores which are borne in tetrads and have the same shape as the megaspores and are sculptured in essentially the same manner. The commissural face usually is marked with three commissural ridges although some have a single ridge. The spores of some species have a prominent wing at the equator. The surface of the microspores also bears distinctive markings such as spines, tubercles, or rugae, but it is difficult to find and to recognize mature material. Photographs of the microspores are included when they are representative and show good detail for the species. Twelve spores were measured for each species. The microspores of *S. rupestris* are similar to the megaspores in that they frequently lack the commissural ridges and an occasional dumb-bell type is found.

The microspores are roughly about one-eighth as large as the megaspores, ranging from 23μ in diameter in several species to 64μ in *S. tortipila*. There is no definite correlation between the size of mega- and microspores of the same species. For example, *S. armata* and *S. selaginoides* have microspores of a similar size while the mode of the megaspores of the former is 0.19 mm. and that of the latter is 0.53 mm. A magnification of at least 400 diameters is necessary to study the surface detail of the microspores, and 70 or 80 diameters is desirable for examination of surface detail of the megaspores.

The microspores are generally more deeply colored than the megaspores, tending toward deep orange or red rather than the lighter yellows, although in some species, as *S. selaginoides*, both mega- and microspores are of the same color.

Slides were prepared by breaking open a microsporangium on a glass slide, adding a drop of lactic acid, and sealing the mount with ringing cement. A lactic acid preparation was more satisfactory than a dry mount, for sculpture not otherwise evident could be distinguished. H. W. Morris, photographer for the University of Minnesota Hospital, photographed the microspores. A homal 3-ocular and a 8-mm. objective were used with a 46-cm. bellows extension of the camera. Illumination was from a carbon arc lamp with a Kaisering green filter. Polychrome plates were used.

The collections studied, for the most part, were identified by such authorities on the genus as Maxon, Van Eseltine, Weatherby, and Wherry. Specimens were examined from the collections of the American Fern Society, Chicago Natural History Museum, Gray Herbarium, University of Minnesota, Missouri Botanical Garden, United States National Museum, and the University of Wisconsin. I wish to express my appreciation to the curators of the herbaria of these institutions who have so kindly lent material for study.

This study has been mainly done at the Missouri Botanical Garden where facilities were generously granted by the Director. The photography was done at the University of Minnesota and the costs incurred supported by the Department of Botany. The problem was initiated at the University of Wisconsin, where a study of *Selaginella* spores was presented as a master's dissertation. I am especially grateful to my husband for the preparation of the photographic unit for the megaspores and for the suggestions and aid given in the study.

SYNOPSIS OF SELAGINELLA IN NORTH AMERICA NORTH OF MEXICO

The following synopsis has been primarily adapted from the current literature, and references are given to the papers upon which it is based. Since there may be some question regarding the disposition of certain species, now generally reduced to synonymy, it was thought desirable to include photographs and discussion of the spores of these. Characters presented in the synopsis allow it to be used to a certain extent as a key. However, the characters are general ones relating to whole groups and are not necessarily without exception. Each species bears the same number in the text and plates as it does in the synopsis.

SUBGENUS EUSELAGINELLA¹

Vegetative leaves uniform; sporophylls uniform.

GROUP OF *S. SELAGINOIDES*. Strobilus cylindric..... 1. *S. SELAGINOIDES* (L.) Link

GROUP OF *S. RUPESTRIS*. Strobilus tetragonus.

- a. Stems typically erect, rooting only at the base.
- b. Setae tortuous.

SUBGROUP OF *S. TORTIPILA*..... 2. *S. TORTIPILA* A. Br.
2. *S. Sherwoodii* Underw. (see Wherry, 1936)

¹The subgenera, groups and series are taken from Walton and Alston (1938).

b. Setae straight.

SUBGROUP OF *S. BIGELOVII*. Megaspores rugose on the outer face.... 3. *S. RUPINCOLA* Underw.
 4. *S. CORYI* Weatherby
 5. *S. BIGELOVII* Underw.
 6. *S. NEOMEXICANA* Maxon

SUBGROUP OF *S. ARENICOLA*. Megaspores smooth or very nearly so on the outer face.....

7. *S. RIDDELLII* Van Eselt.
 8. *S. ARENICOLA* Underw.
 8. *S. funiformis* Van Eselt. (see Clausen, 1946)
 9. *S. ACANTHONOTA* Underw.
 9. *S. floridana* Maxon (see Clausen, 1946)

a. Stems prostrate, rooting throughout.

c. Stems radially symmetrical.

SUBGROUP OF *S. OREGANA*. Stems elongate, slender, branches remote. (see Weatherby, 1944).....

10. *S. OREGANA* D. C. Eaton
 11. *S. UNDERWOODII* Hieron.
 12. *S. MUTICA* D. C. Eaton
 13. *S. CINEASCENS* A. A. Eaton

SUBGROUP OF *S. RUPESTRIS*. Stems short, stout, branches congested..

14. *S. WATSONII* Underw.
 15. *S. STANLEYI* Maxon
 16. *S. LEUCOBRYOIDES* Maxon
 17. *S. WALLACEI* Hieron.
 18. *S. SIBIRICA* (Milde) Hieron.
 19. *S. ASPRELLA* Maxon
 20. *S. DENSA* Rydb.
 21. *S. RUPESTRIS* (L.) Spring
 22. *S. SCOPULORUM* Maxon
 23. *S. WRIGHTII* Hieron.

c. Stems strongly dorsiventral.

SUBGROUP OF *S. HANSENI*. Vegetative leaves uniform or nearly so..

24. *S. SHELDONII* Maxon
 25. *S. HANSENI* Hieron.

SUBGROUP OF *S. PARISHII*. Vegetative leaves dimorphous. (see Weatherby, 1943a).....

26. *S. ARIZONICA* Maxon
 27. *S. EKEMOPHILA* Maxon

SUBGENUS STACHYGYNANDRUM

Vegetative leaves dimorphous, sporophylls uniform.

SERIES DECUMBENTES. Widely creeping, prostrate, stems rooting throughout.....

28. *S. DOUGLASII* (Hook. & Grev.) Spring
 29. *S. ARMATA* Baker
 30. *S. APODA* (L.) Fern. (*S. Indoviciana* A. Br.)

1949]

TRYON—SELAGINELLA SPORES

417

SERIES CIRCINATAE. Tufted xerophytes, ascendent, rooted only at the base.. 31. *S. LEPIDOPHYLLA*
(Hook. & Grev.)
Spring
32. *S. PILIFERA* A. Br.
(*S. Pringlei* Baker—
see Morton, 1939, and
Weatherby, 1943b)

DESCRIPTION

SUBGENUS EUSELAGINELLA

GROUP OF *S. SELAGINOIDES*.—1. *S. SELAGINOIDES* (L.) Link.

Pl. 23, fig. 1.

Megaspores Barium Yellow (yellow, green-tinged); 0.48–0.52–0.53 mm. in diameter, 18 spores measured. *Microspores* Barium Yellow (yellow, green-tinged); 26–34 μ in diameter.

GROUP OF *S. RUPESTRIS*.—SUBGROUP OF *S. TORTIPILA*.—

The two members of this group cannot be distinguished on the basis of spores. This would agree with Wherry's (1936) conclusion that *S. Sherwoodii* is merely an ecological form of *S. tortipila*. The megaspores of *S. Sherwoodii* in the collection examined are strongly tuberculate-rugose. Those of *S. tortipila* are of a similar pattern of sculpture and some are less prominently marked.

2. *S. TORTIPILA* A. Br.

Pl. 23, fig. 2.

Megaspores Straw Yellow to Lemon Chrome (lemon-yellow); 0.25–0.34–0.41 mm. in diameter, 26 spores measured. Some spores are more prominently rugose on the outer face than in fig. 2b. *Microspores* Pinard Yellow (pale yellow); 41–64 μ in diameter.

2. *S. Sherwoodii* Underw.

Pl. 23, fig. 2.

Megaspores Apricot Yellow (pale orange); 0.32–0.40 mm. in diameter, 9 spores measured. Some spores are less prominently tuberculate-rugose on the outer face than in fig. 2b. *Microspores* Apricot-Yellow (pale orange); 38–63 μ in diameter.

SUBGROUP OF *S. BIGELOVII*.—

Megaspores of *S. rupincola* show a marked variation in prominence of sculpturing. Fig. 3b represents an extreme phase with a well-marked equatorial ring. For the most part, the megaspores examined are sculptured to a less degree as illustrated in fig. 3a, but with a more strongly pronounced equatorial ring. Megaspores of *S. Bigelovii* examined are finely rugose and usually bear an equatorial ring. Some megaspores are marked with subechinate, lace-like prominences which can be seen along the margins of the spores illustrated.

Commissural face of megaspores with moderately coarse rugae; outer face rugose to rugose-tuberculate, ridges low and crowded, areole narrow if present..... 3. *S. RUPINCOLA*
Commissural face of megaspores with fine rugae; outer face with low, obscure rugae, areolae small, scarcely distinct from the low, rounded ridges.. 5. *S. BIGELOVII*

3. *S. RUPINCOLA* Underw.

Pl. 24, fig. 3.

Megaspores Apricot Yellow (pale orange); 0.19–0.29–0.34 mm. in diameter, 29 spores measured. *Microspores* Deep Chrome (bright orange); 38–64 μ in diameter.

4. *S. CORYI* Weath. Am. Fern Jour. 36:51–53. 1946.

Spores of this species were not available for photography but two megaspores from the TYPE have been examined. They are rather similar to those of *S. rupincola* except that they lack an equatorial ring. They are about 0.4 mm. in diameter and Apricot Yellow (pale orange). The rugae are prominent on the outer face and there are distinct areoles between the rugae.

5. *S. BIGELOVII* Underw.

Pl. 24, fig. 5.

Megaspores Apricot Yellow (pale orange); 0.25–0.34–0.40 mm. in diameter, 49 spores measured. *Microspores* Apricot Yellow (pale orange); 38–49 μ in diameter.

6. *S. NEOMEXICANA* Maxon.

Megaspores unknown.

SUBGROUP OF *S. ARENICOLA*.—

The members comprising this group are difficult to distinguish on the basis of the spores. Clausen (1946) has recognized three species and remarked that of these *S. arenicola* and *S. acanthonota* are not wholly separable. The commissural face is more strongly marked than the outer face in all of the species. However, the sculpturing is rather variable and there appears to be no marked character which distinguishes the species except the degree of prominence of the sculpturing.

The megaspores of *S. Riddellii* are more strongly marked on the outer face than those of the other species. In the collections studied the megaspores of *S. acanthonota* are as prominently rugose-reticulate on the commissural face as those of *S. Riddellii*, and phases of sculpture on the megaspores of *S. acanthonota* and *S. arenicola* are indistinguishable.

Megaspores rugose on outer face..... 7. *S. RIDDELLII*
Megaspores smooth on outer face.....

Scarcely rugose on the commissural face..... 8. *S. ARENICOLA*

Rugose to rugose-tuberculate on commisural face..... 8. *S. funiformis*

9. *S. ACANTHONOTA*

9. *S. floridana*

7. *S. RIDDELLII* Van Eseltine.

Pl. 24, fig. 7.

Megaspores Lemon Chrome (lemon yellow); 0.21–0.32 & 0.38–0.46 mm. in diameter, 16 spores measured. The outer face is usually more prominently rugose than in fig. 7b. *Microspores* Apricot Yellow (pale orange); 34–53 μ in diameter.

8. *S. ARENICOLA* Underw.

Pl. 24, fig. 8.

Megaspores White to Apricot Yellow (pale orange); 0.25–0.29–0.42 mm. in diameter, 35 spores measured. The outer face is smooth or minutely punctate. *Microspores* Apricot Yellow to Deep Chrome (pale to bright orange); 34–47 μ in diameter.

8. *S. funiformis* Van Eseltine.

Pl. 25, fig. 8.

Megaspores Straw Yellow to Pinard Yellow (pale yellow); 0.21–0.34 mm. in diameter, 6 spores measured. The spores examined are similar in pattern of marking to those of *S. arenicola* but are of a deeper yellow. *Microspores* Deep Chrome (bright orange); 30–41 μ in diameter.

9. *S. ACANTHONOTA* Underw.

Pl. 25, fig. 9.

Megaspores White to Lemon Chrome (lemon yellow); 0.29–0.36–0.42 mm. in diameter, 28 spores measured. The pattern of sculpture is similar but the degree of prominence varies between that represented in fig. 9a and 9b. *Microspores* Deep Chrome (bright orange); 34–45 μ in diameter.

9. *S. floridana* Maxon.

Pl. 25, fig. 9.

Megaspores White to Lemon Chrome (lemon yellow); 0.19–0.32–0.40 mm. in diameter, 36 spores measured. *Microspores* Deep Chrome (bright orange); 32–53 μ in diameter.

SUBGROUP OF *S. OREGANA*.—

The group of *S. oregana* as treated by Weatherby (1944) includes several Mexican species and is characterized on the basis of habit. The spores of the species treated here are all distinct and do not appear to indicate relationships between the species.

- a. Commissural face of megaspore more prominently rugose than outer face, commissural ridges connected by equatorial ring or free.
- b. Commissural face delicately rugose, commissural ridges thin and delicate.
- c. Outer face slightly reticulate, meshes forming small areolae scarcely more distinct than those of the commissural face..... 10. *S. OREGANA*
- c. Outer face strongly reticulate, meshes forming broad, shallow areolae more distinct than those on the commissural face..... 11. *S. UNDERWOODII*
- b. Commissural face coarsely and remotely rugose, commissural ridges broad and coarse; outer face lightly rugose to smooth..... 12. *S. MUTICA*
- a. Commissural face of megaspores lightly rugose, less prominently sculptured than outer face, commissural ridges connected by a prominent, thin equatorial ring..... 13. *S. CINERASCENS*

10. *S. OREGANA* D. C. Eaton.

Pl. 25, fig. 10.

Megaspores Pinard Yellow (pale yellow); 0.27–0.32–0.36 mm. in diameter, 25 spores measured. Some spores bear cross ridges connecting the commissural ridges. *Microspores* Pinard Yellow (pale yellow); 41–56 μ in diameter.

11. *S. UNDERWOODII* Hieron.

Pl. 26, fig. 11.

Megaspores Apricot Yellow (pale orange); 0.27–0.36–0.42 mm. in diameter, 38 spores measured. *Microspores* Deep Chrome (bright orange); 30–45 μ in diameter.

12. *S. MUTICA* D. C. Eaton.

Pl. 26, fig. 12.

Megaspores Apricot Yellow (pale orange); 0.21–0.29–0.42 mm. in diameter, 31 spores measured. Some spores bear an equatorial ring; some are more strongly rugose-reticulate than fig. 12a. *Microspores* Apricot Yellow (pale orange); 30–53 μ in diameter.

13. *S. CINERASCENS* A. A. Eaton.

Pl. 26, fig. 13.

Megaspores Pinard Yellow (pale yellow); 0.32–0.37–0.38 mm. in diameter, 16

spores measured. *Microspores* Apricot Yellow (pale orange); 38–53 μ in diameter.

SUBGROUP OF *S. RUPESTRIS*.—

The subgroup of *S. rupestris* includes the largest number and the most perplexing species of the subgenus. Several of the species are undoubtedly aggregate groups which need to be extensively collected and critically examined. Maxon (1920, 1921) has investigated some of these and has remarked on relationships between them, but for the most part a natural series has not been worked out.

There is a remarkable similarity between the pattern of sculpture of the megaspores of some of the species. The megaspores of *S. asprella* and one phase of the megaspores of *S. densa* cannot be distinguished. However, there is much variation in the spore sculpture between collections of *S. densa*. Some collections of *S. Watsoni* have megaspores scarcely rugose and very similar in pattern to those of *S. Standleyi*; others have prominently marked spores rather like those of *S. scopulorum*. The megaspores of *S. Wallacei* are variously sculptured but frequently characterized by an equatorial ring.

- a. Megaspores 4 per sporangium; 3 commissural ridges.
b. Outer face obscurely rugose-reticulate to nearly smooth.
c. Commissural face finely rugose-reticulate..... 14. *S. WATSONI*
- c. Commissural face with coarse, low rugae..... 15. *S. STANLEYI*
- b. Both faces strongly rugose to rugose-tuberculate.
d. Commissural face with coarse, remote rugae; outer face strongly reticulate, surface of the areolae broad and smooth..... 16. *S. LEUCOBRYOIDES*
- d. Commissural face with delicate, compact rugae; outer face with areolae small or scarcely apparent.
e. Commissural face strongly rugose to rugose-reticulate; nearly all rugae on outer face joined in a net forming areolae of moderate size.
f. Equatorial ring usually present..... 17. *S. WALLACEI*
- f. Without equatorial ring..... 14. *S. WATSONI*
- e. Both faces with prominent flexuous rugae which have free ends, areolae narrow if present..... 18. *S. SIBIRICA*
- a. Megaspores 2 per sporangium; commissural ridges lacking or a single ridge present..... 22. *S. SCOPULORUM*
- 23. *S. WRIGHTII*
- 21. *S. RUPESTRIS*

14. *S. WATSONI* Underw.

Pl. 26, fig. 14.

Megaspores Apricot Yellow (pale orange); 0.27–0.40–0.50 mm. in diameter, 75 spores measured. The commissural ridges are usually straight and the commissural face somewhat less prominently sculptured than fig. 14a. *Microspores* Deep Chrome (bright orange); 30–53 μ in diameter.

15. *S. STANLEYI* Maxon.

Pl. 27, fig. 15.

Megaspores Apricot Yellow (pale orange); 0.34–0.40–0.48 mm. in diameter, 24 spores measured. Some spores are more prominently rugose than fig. 15. *Microspores* Apricot Yellow (pale orange); 26–41 μ in diameter.

16. *S. LEUCOBRYOIDES* Maxon.

Pl. 27, fig. 16.

Megaspores Apricot Yellow (pale orange); 0.32–0.47 mm. in diameter, 8 spores measured. *Microspores* Flame Scarlet (red orange); 38–56 μ in diameter.

1949]

17. *S. WALLACEI* Hieron.

Pl. 27, fig. 17.

Megaspores Apricot Yellow (pale orange); 0.27–0.34–0.38 mm. in diameter, 51 spores measured. Some spores are less prominently sculptured than fig. 17, and some are without an equatorial ring. *Microspores* Deep Chrome (bright orange); 38–49 μ in diameter.

18. *S. SIBIRICA* (Milde) Hieron.

Pl. 27, fig. 18.

Megaspores Pinard Yellow to Apricot Yellow (pale yellow to pale orange); 0.38–0.40–0.42 mm. in diameter, 5 spores measured. The commissural ridges are usually twice as long as those in fig. 18a. *Microspores* Deep Chrome (bright orange); 38–49 μ in diameter.

19. *S. ASPRELLA* Maxon.

Pl. 28, fig. 19.

Megaspores Straw Yellow to Apricot Yellow (pale orange); 0.29–0.34–0.38 mm. in diameter, 6 spores measured. Some spores have an equatorial ring. *Microspores* Pinard Yellow to Deep Chrome (bright yellow to bright orange); 34–53 μ in diameter.

20. *S. DENSA* Rydb.

Pl. 28, fig. 20.

Megaspores Apricot Yellow (pale orange); 0.36–0.40–0.50 mm. in diameter, 48 spores measured. The spores photographed are from type material and illustrate the pattern of sculpture in several of the collections studied. *Microspores* Deep Chrome (bright orange); 34–49 μ in diameter.

21. *S. RUPESTRIS* (L.) Spring.

Pl. 28, fig. 21.

Megaspores Deep Chrome (bright orange); 0.32–0.46–0.53 mm. in diameter, 53 spores measured. The sculpture of the spores examined is generally of the same pattern, varying in the prominence of reticulation. *Microspores* Apricot Yellow (pale orange); spores monolete, 49–75 μ in greatest dimension.

22. *S. SCOPULORUM* Maxon.

Pl. 28, fig. 22.

Megaspores Deep Chrome (bright orange); 0.32–0.42–0.48 mm. in diameter, 35 spores measured. *Microspores* Apricot Yellow (pale orange); 34–56 μ in diameter.

23. *S. WRIGHTII* Hieron.

Pl. 29, fig. 23.

Megaspores Apricot Yellow to Deep Chrome (pale to bright orange); 0.18–0.25–0.55 mm. in diameter, 44 spores measured. There is considerable variation in size of spores of this species, since one large spore may develop at the expense of three small spores within a megasporangium. The pattern of sculpture of the spores is generally similar. *Microspores* Deep Chrome (bright orange); 34–56 μ in diameter.

SUBGROUP OF *S. HANSENI*.—

The two species of this subgroup are allied on the basis of strongly dorsiventral stems and uniform leaves. The spores are distinctive for each species.

Commissural face of megaspores without equatorial ring; strongly reticulate
on outer face.....

24. *S. SHELDONI*

Commissural face of megaspores with prominent equatorial ring; lightly
rugose on outer face.....

25. *S. HANSENI*

24. *S. SHELDONI* Maxon.

Pl. 29, fig. 24.

Megaspores Deep Chrome (bright orange); 0.34-0.36-0.44 mm. in diameter, 28 spores measured. *Microspores* Deep Chrome (bright orange); 34-45 μ in diameter.

25. *S. HANSENI* Hieron.

Pl. 29, fig. 25.

Megaspores Lemon Chrome (lemon yellow); 0.29-0.36-0.42 mm. in diameter, 40 spores measured. *Microspores* Apricot Yellow (pale orange); 38-49 μ in diameter.

SUBGROUP OF *S. PARISHII*.—

Two members of this group are Mexican and are not treated here. The megaspores of *S. eremophila* are for the most part more prominently sculptured than the megaspores of *S. arizonica*. In both species a single, large megaspore and three small spores may be found within a sporangium.

Commissural face of megaspore finely rugose-reticulate; scarcely marked with equatorial ring; outer face coarsely reticulate to smooth..... 26. *S. ARIZONICA*
Commissural face of megaspore with sharp, projecting rugae, prominent equatorial ring; outer face deeply rugose-reticulate..... 27. *S. EREMOPHILA*

26. *S. ARIZONICA* Maxon.

Pl. 29, fig. 26.

Megaspores Apricot Yellow (pale orange); 0.25-0.32-0.46 mm. in diameter, 36 spores measured. Some spores are more prominently marked than fig. 26b; some have an obscure equatorial ring. *Microspores* Deep Chrome (bright orange); 23-38 μ in diameter.

27. *S. EREMOPHILA* Maxon.

Pl. 29, fig. 27.

Megaspores Pinard Yellow (pale yellow); 0.23-0.34-0.50 mm. in diameter, 25 spores measured. *Microspores* Deep Chrome (bright orange); 38-53 μ in diameter.

SUBGENUS STACHYGYNANDRUM

The species included in this study belonging to this subgenus are all characterized by strikingly distinct spores. The microspores are as strongly marked as the megaspores. The microspores of *S. apoda* and *S. Douglasii* have a pebbled appearance, those of *S. armata* are beset with papillae and those of *S. pilifera* have globules of a waxy substance adhering to them.

SERIES DECUMBENTES.—

Megaspores less than 0.22 mm. in diameter; deep yellow to orange; obscurely rugose to nearly smooth..... 29. *S. ARMATA*

Megaspores more than 0.36 mm. in diameter; straw-yellow or lighter with a green-tinge; strongly marked.

Megaspores granular to tuberculate..... 28. *S. DOUGLASHII*

Megaspores marked with prominent, thin, free rugae..... 30. *S. APODA*

28. *S. DOUGLASHII* (Hook. & Grev.) Spring.

Pl. 30, fig. 28.

Megaspores Straw Yellow; 0.36-0.38-0.40 mm. in diameter, 7 spores measured. *Microspores* Deep Chrome (bright orange); 23-41 μ in diameter.

29. *S. ARMATA* Baker.

Pl. 30, fig. 29.

Megaspores Deep Chrome (bright orange); 0.15-0.19-0.21 mm. in diameter, 15 spores measured. *Microspores* Flame Scarlet (red orange); 26-34 μ in diameter.

24. 30. *S. APODA* (L.) Fern.

Pl. 30, fig. 30.

28. *Megaspores* Barium Yellow (yellow, green-tinged); 0.34–0.36 mm. in diameter,
ter. 7 spores measured. *Microspores* Flame Scarlet (red orange); 23–34 μ in diameter.
25. SERIES *CIRCINATAE*.—ter, in
in
gat-
the
ree
26. 31. *S. LEPIDOPHYLLA* (Hook. & Grev.) Spring. Pl. 30, fig. 31.27. *Megaspores* Deep Chrome (bright orange); 0.23–0.29–0.42 mm. in diameter, 23
spores measured. *Microspores* adhere in tetrads which are Flame Scarlet (red
ree orange).28. 32. *S. PILIFERA* A. Br. Pl. 30, fig. 32.
ter. *Megaspores* Straw Yellow to Pinard Yellow (pale orange); 0.25–0.29 mm. in
in diameter, 11 spores measured. Some spores have an equatorial ring. *Microspores*
gat- Flame Scarlet (red orange); 26–38 μ in diameter.the
ree
BIBLIOGRAPHY

Baker, J. G. (1887). Handbook of the fern allies. London.
 Broun, M. (1938). Index to North American ferns. Orleans, Mass.
 Clausen, R. T. (1946). *Selaginella*, subgenus *Euselaginella*, in the southeastern United States. Am. Fern Jour. 36:65–82.
 Hieronymus, G. (1900). *Selaginellarum* species novae vel non satis cognitae. I. Hedwigia 39:290–320.
 Lyon, F. M. (1901). A study of the sporangia and gametophytes of *Selaginella apus* and *Selaginella rupestris*. Bot. Gaz. 32:124–141, 170–194.
 — (1905). The spore coats of *Selaginella*. Ibid. 40:285–295.
 Maxon, W. R. (1918). A new *Selaginella* from Oklahoma and Texas. Proc. Biol. Soc. Wash. 31:171–172.
 — (1920). New *Selaginellas* from the western United States. Smithson. Misc. Coll. 72:1–10.
 — (1921). Notes on American ferns—XVII. Am. Fern Jour. 11:34–39.
 — (1923). Notes on American ferns—XIX. Ibid. 13:73–75.
 Morton, C. V. (1939). Our southwestern resurrection plants. Ibid. 29:14–16.
 Reeve, R. M. (1935). The spores of the genus *Selaginella* in north central and north eastern United States. Rhodora 37:341–345.
 Ridgway, Robert (1912). Color standards and color nomenclature. Washington, D. C.
 Selling, O. H. (1946). Studies in Hawaiian pollen statistics. Pt. I. Bishop Mus. Spec. Publ. 37.
 Underwood, L. M. (1898). *Selaginella rupestris* and its allies. Bull. Torrey Bot. Club 25:125–133.
 — (1901). A changed conception of species. Fern Bull. 9:49–53.
 Van Eseltine, G. P. (1918). The allies of *Selaginella rupestris* in the southeastern United States. Contr. U. S. Nat. Herb. 20:159–172.
 Walton, J., and A. H. G. Alston (1938). Lycopodiinae in Verdoorn, Manual of Pteridology, pp. 503–506.
 Weatherby, C. A. (1943a). The group of *Selaginella Parisbii*. Am. Fern Jour. 33:113–119.
 — (1943b). Selaginellaceae, in Johnston, I. M., Plants of northern Mexico, I. Jour. Arn. Arb. 24:325–329.
 — (1944). The group of *Selaginella oregana* in North America. Ibid. 25:407–419.
 — (1946). A new *Selaginella* from western Texas. Am. Fern Jour. 36:51–53.
 Wherry, E. T. (1936). Observations on *Selaginella tortipila*. Jour. So. Appalach. Bot. Club 1:65–69.

EXPLANATION OF PLATE

In this and the following plates, which are reproductions of photographs, the magnification for the megaspores is 85 diameters and for the microspores 450 diameters.

PLATE 23

Fig. 1. *S. SELAGINOIDES*: *Butters & Holway*, Alberta, 1905 (Univ. Minn.). 1a. Commissural face of megaspore. 1b. Outer face of megaspore.

Fig. 2. *S. TORTIPILA*: *Donnell-Smith*, South Carolina, 1881 (Chicago Nat. Hist. Mus.). 2a. Commissural face of megaspore. 2b. Outer face of a moderately marked spore.

Fig. 2. *S. Sherwoodii*: *Donnell-Smith*, North Carolina, 1882 (Mo. Bot. Gard.). 2a. Commissural face of megaspore. 2b. Outer face of a strongly marked megaspore. 2c. Microspore.



S. funiformis



S. acanthonota

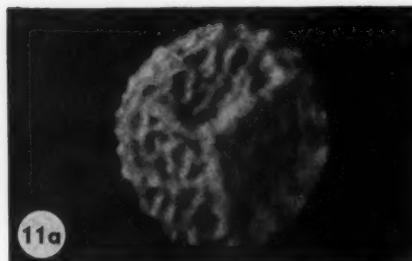


S. floridana

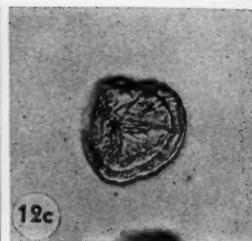


S. oregana

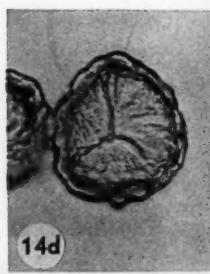
TRYON — SELAGINELLA SPORES



S. UNDERWOODII



S. MUTICA



S. CINERASCENS



S. WATSONI

TRYON — SELAGINELLA SPORES

[Vol. 36, 1949]

EXPLANATION OF PLATE

PLATE 24

Fig. 3. *S. RUPINCOLA*: 3a. Commissural face of megaspore, *Goodding*, Arizona, 1921 (Chicago Nat. Hist. Mus.). 3b. Commissural face of prominently sculptured megaspore, *Wooton*, New Mexico, 1907 (Univ. Minn.). 3c. Outer face of megaspore, from the same specimen as 3a.

Fig. 5. *S. BIGELOVII*: 5a. Commissural face of megaspore without prominent equatorial ring, *Rose* 34495, California, 1932 (Chicago Nat. Hist. Mus.). 5b. Outer face of megaspore, *Grant & Wheeler*, California, 1904 (Univ. Minn.). 5c. Microspore from the same specimen as 5a.

Fig. 7. *S. RIDDELLII*: *Cory* 41009, Texas, 1943 (Gray Herb.). 7a. Commissural face of megaspore. 7b. Outer face of a lightly marked megaspore. 7c. Microspore.

Fig. 8. *S. ARENICOLA*: *Deam* 63923, Florida, 1946 (Mo. Bot. Gard.). 8a. Commissural face of megaspore. 8b. Outer face of megaspore. 8c. Microspore.

EXPLANATION OF PLATE

PLATE 25

Fig. 8. *S. funiformis*: O'Neill 7580, Florida, 1933 (Chicago Nat. Hist. Mus.).
8a. Commissural face of megaspore. 8b. Outer face of megaspore.

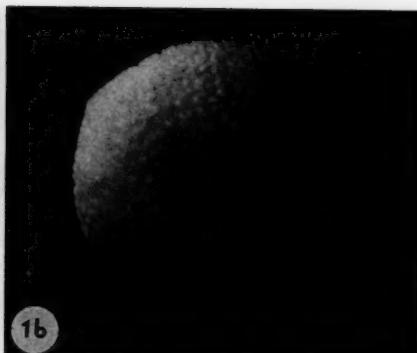
Fig. 9. *S. ACANTHONOTA*: 9a. Commissural face of a lightly marked megaspore, Pyron & McVaugh 3101, Georgia, 1938 (Mo. Bot. Gard.). 9b. Commissural face of a prominently marked megaspore, Harper 1957, Georgia, 1903 (Mo. Bot. Gard.). 9c. Outer face of megaspore, from same specimen as 9a.

Fig. 9. *S. floridana*: Nash 1449, Florida, 1894, Isotype (Chicago Nat. Hist. Mus.).
9a. Commissural face of megaspore. 9b. Outer face of megaspore.

Fig. 10. *S. OREGANA*: Piper, Washington, 1893 (Univ. Minn.). 10a. Commissural face of megaspore. 10b. Outer face of megaspore. 10c. Microspore.

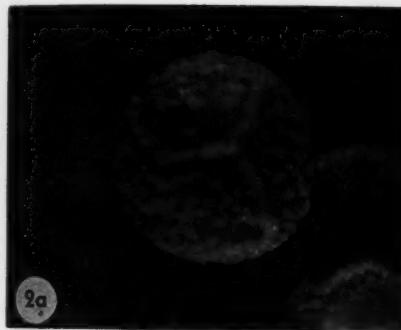


1a

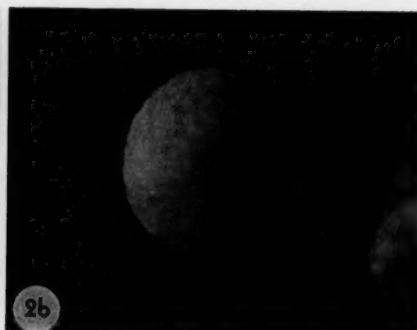


1b

S. SELAGINOIDES



2a



2b

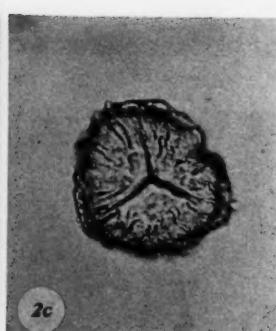
S. TORTIPILA



2a



2b



2c

S. Sherwoodii

TRYON — SELAGINELLA SPORES



3a

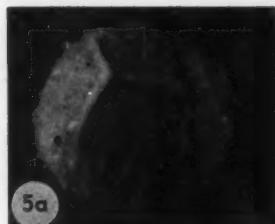


3b



3c

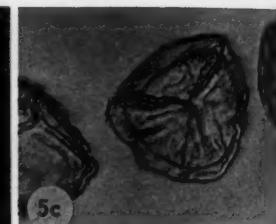
S. RUPINCOLA



5a

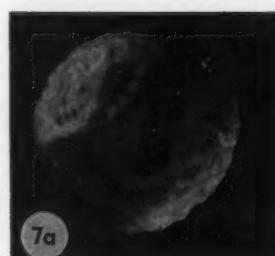


5b



5c

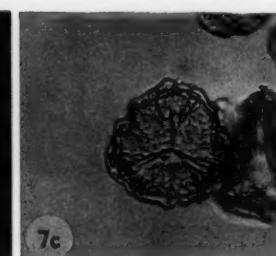
S. BIGELOVII



7a

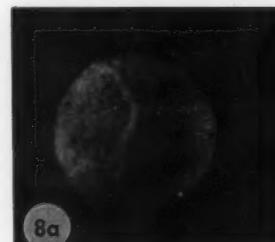


7b



7c

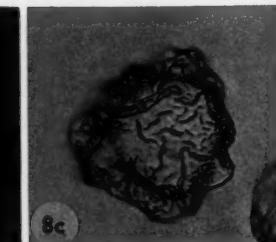
S. RIDDELLII



8a



8b



8c

S. ARENICOLA

TRYON—SELAGINELLA SPORES

EXPLANATION OF PLATE

PLATE 26

Fig. 11. *S. UNDERWOODII*: 11a. Commissural face of megaspore (var. *dolichotricha* Weath.), Metcalfe 991, New Mexico (Mo. Bot. Gard.). 11b. Outer face of megaspore, Clark 8968, Arizona, 1940 (Mo. Bot. Gard.).

Fig. 12. *S. MUTICA*: Drouet, Richards & Rubinstein 4097, Colorado, 1941 (Mo. Bot. Gard.). 12a. Commissural face of a lightly marked spore without an equatorial ring. 12b. Outer face of megaspore. 12c. Microspore.

Fig. 13. *S. CINERASCENS*: Abrams 3399, California, 1903 (Chicago Nat. Hist. Mus.). 13a. Commissural face of megaspore. 13b. Outer face of megaspore.

Fig. 14. *S. WATSONI*: Maguire, Hobson & Maguire 14729, Utah, 1936 (U. S. Nat. Herb.). 14a. Commissural face of a prominently marked megaspore with unusual flexuose commissural ridges. 14b. Outer face of megaspore. 14c. Outer face of megaspore with large areolae. 14d. Microspore.

EXPLANATION OF PLATE

PLATE 27

Fig. 15. *S. STANDLEYI*: *Wherry*, Colorado (U. S. Nat. Herb. 1730847). 15a. Commissural face of a lightly marked megaspore. 15b. Outer face of a lightly marked megaspore.

Fig. 16. *S. LEUCOBRYOIDES*: *Munz & Harwood* 3789, California, 1920, Isotype (Chicago Nat. Hist. Mus.). 16a. Commissural face of a lightly marked megaspore. Note microspore attached near end of one commissural ridge. 16b. Outer face of microspore.

Fig. 17. *S. WALLACEI*: *Constance & Rollins* 998, Washington, 1935 (Univ. Minn.). 17a. Commissural face of a prominently marked megaspore with prominent equatorial ring. 17b. Outer face of a prominently marked megaspore.

Fig. 18. *S. SIBIRICA*: *Porsild* 159, Alaska, 1926 (Gray Herb.). 18a. Commissural face of a megaspore with unusually short commissural ridges. 18b. Outer face of megaspore.

EXPLANATION OF PLATE

PLATE 28

Fig. 19. *S. ASPRELLA*: *Johnston* 1807, California, 1917, Paratype (U. S. Nat. Herb.).
19a. Commissural face of megaspore. 19b. Outer face of megaspore. 19c. Microspore.

Fig. 20. *S. DENSA*: *Rydberg* & *Bessey* 3517, Montana, 1897, Isotype (Chicago Nat. Hist. Mus.). 20a. Commissural face of megaspore. 20b. Outer face of prominently marked megaspore.

Fig. 21. *S. RUPESTRIS*: 21a. Commissural face of a megaspore with a single, straight commissural ridge: *B. C. Taylor* 1573, Wisconsin, 1892 (Univ. Minn.). 21b. Outer face of megaspore: *Umbach* 5166, Indiana, 1910 (Mo. Bot. Gard.). 21c. Dumb-bell megaspore, from same specimen as 21a. 21d. Microspore, *Tryon* & *Tryon* 5005, Wisconsin, 1947 (Mo. Bot. Gard.).

Fig. 22. *S. SCOPULORUM*: 22a. Commissural face of megaspore, *Shaw* 902, British Columbia, Isoparatype (Univ. Minn.). 22b. Outer face of megaspore, *Umbach* 856, Montana, Isoparatype (Chicago Nat. Hist. Mus.).

EXPLANATION OF PLATE

PLATE 29

Fig. 23. *S. WRIGHTII*: *Reverchon*, Texas, 1883 (U. S. Nat. Herb.). 23a. Commissural face of megaspore. 23b. Outer face of megaspore.

Fig. 24. *S. SHELDONI*: *Cory 30143*, Texas, 1938 (Mo. Bot. Gard.). 24a. Commissural face of megaspore. 24b. Outer face of megaspore. 24c. Microspore.

Fig. 25. *S. HANSENI*: *Heller 11802*, California, 1915 (Chicago Nat. Hist. Mus.). 25a. Commissural face of megaspore. 25b. Outer face of megaspore.

Fig. 26. *S. ARIZONICA*: *Goodding*, Arizona, 1921 (Chicago Nat. Hist. Mus.). 26a. Commissural face of megaspore. 26b. Outer face of a lightly marked megaspore.

Fig. 27. *S. EREMOPHILA*: *Cook*, California, 1921 (U. S. Nat. Herb.). 27a. Commissural face of a megaspore with obscure equatorial ring. 27b. Outer face of megaspore.



S. STANDLEYI



S. LEUCOBRYOIDES

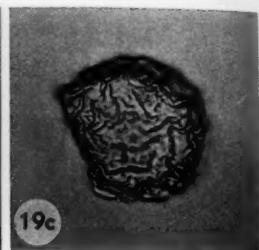
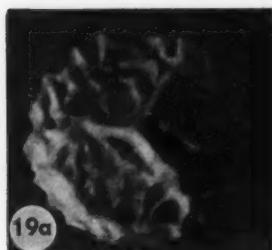


S. WALLACEI

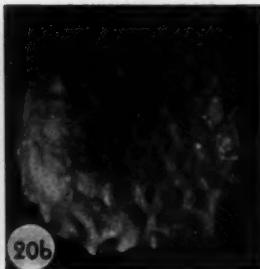


S. SIBIRICA

TRYON — SELAGINELLA SPORES



S. ASPRELLA



S. DENSA

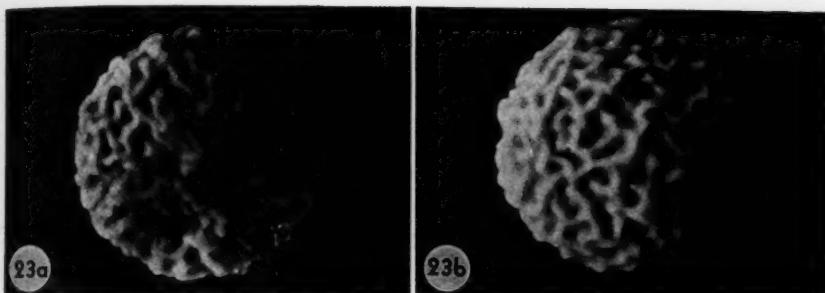


S. SCOPULORUM



S. RUPESTRIS

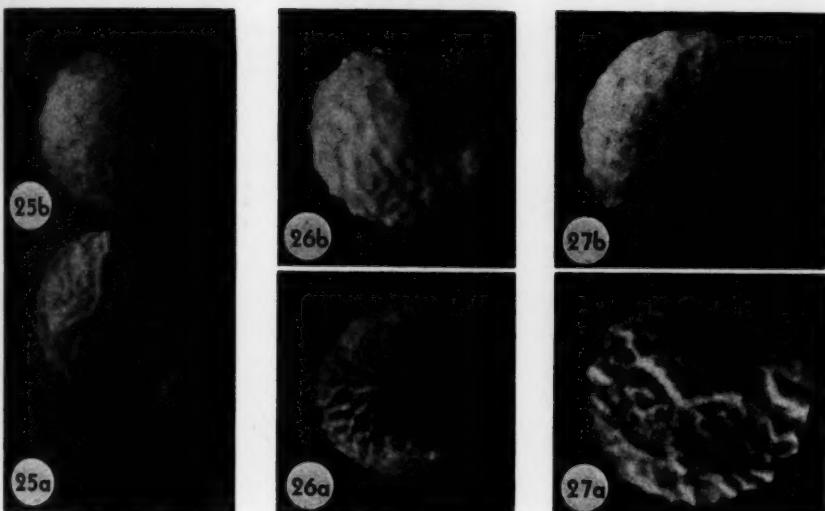
TRYON — SELAGINELLA SPORES



S. WRIGHTII



S. SHELDONI



S. HANSENI

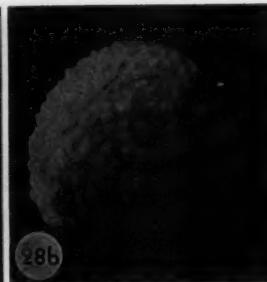
S. ARIZONICA

S. EREMOPHILA

TRYON — SELAGINELLA SPORES



28a



28b



28c

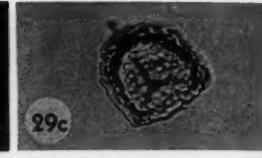
S. DOUGLASII



29a

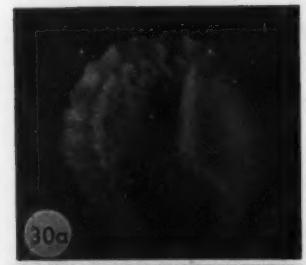


29b



29c

S. ARMATA



30a



31a



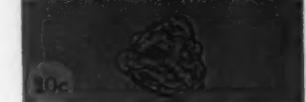
32a



30b



31b



30c



31c

S. APODA

S. LEPIDOPHYLLA

S. PILIFERA

TRYON — SELAGINELLA SPORES

[Vol. 36, 1949]

EXPLANATION OF PLATE

PLATE 30

Fig. 28. *S. DOUGLASHI*: *Peck*, Oregon, 1914 (Mo. Bot. Gard.). 28a. Commissural face of megaspore. 28b. Outer face of megaspore. 28c. Microspore.

Fig. 29. *S. ARMATA*: *Small & Carter*, Florida, 1903 (Univ. Minn.). 29a. Commissural face of megaspore. 29b. Outer face of megaspore. 29c. Microspore.

Fig. 30. *S. APODA*: 30a. Commissural face of megaspore, *Ruth*, Pennsylvania, 1890 (Univ. Minn.). 30b. Outer face of megaspore, from same specimen as 30a. 30c. Microspore, *E. L. Nielson 1564*, Massachusetts, 1932 (Univ. Minn.).

Fig. 31. *S. LEPIDOPHYLLA*: *E. J. Palmer 11366*, Texas, 1917 (Mo. Bot. Gard.). 31a. Commissural face of megaspore. 31b. Outer face of megaspore.

Fig. 32. *S. PILIFERA*: *C. H. Mueller 8257*, Texas (Mo. Bot. Gard.). 32a. Commissural face of megaspore without equatorial ring. 32b. Outer face of megaspore. 32c. Microspore.

THE CYTOLOGY OF PAPHIOPEDILUM MAUDIAE HORT.¹

HENRY A. MCQUADE

STATEMENT OF THE PROBLEM

The hybrid *Paphiopedilum Maudiae* Hort. is the offspring of *Paphiopedilum callosum* var. *Sanderae* and *P. Lawrenceanum* var. *Hyeanum*. It has been used in relatively few crosses despite its quality, and its offspring have rarely, if ever, been able to exceed it. It was felt that an orchid of such superiority which produced little and often no seed should be examined cytologically to ascertain, if possible, the causes of its sterility. Accordingly, cytological examination was made of the parents and the hybrid and some observations were made on somatic tissues of certain related species.

I. PAPHIOPEDILUM Pfitz.

Paphiopedilum was originally incorporated in the genus *Cypripedium* described by Linnaeus. From *Cypripedium* were later extracted the three other genera of the Tribe CYPRIPEDILINAE as they are generally accepted today; the residue of the large genus continues under Linnaeus' original designation. The orchid-grower continues to refer to various species of *Paphiopedilum* as "Cypripedium," and the confusion oftentimes extends to the remaining genera.

Linnaeus arrived at the name *Cypripedium* in an effort to latinize what he thought were the proper Greek words for the "Slipper of Venus." These are *Kυρpis* (Latin *Veneris*) and *ποδον* (*calcens*). The last, however, does not signify the Latin *calceus*, or shoe, but rather is the word for a small foot. Ascherson² changed the generic name to *Cypripedium* (*pedilum* representing the latinization of the Greek equivalent of *calcetus*), and this was adopted by Pfitzer (1886) and published as such. Buser (1894) has concluded that both names represent the latinization of "very mediocre Greek," but that by virtue of priority *Cypripedium* would be correct: Since Linnaeus had used *Cypripedium* consistently in both 'Species Plantarum' and 'Genera Plantarum' Pfitzer would have no right under present-day rules to suggest a change.

Selenipedium was changed to *Selenipedium* by Pfitzer in 1886 on the same basis that the change was made in *Cypripedium*. The genus was originally described as *Selenipedium* by Reichenbach filius (1859) who used this spelling consistently. On the basis of priority as determined by the present-day rules of nomenclature, *Selenipedium* is the proper expression.

The use of *Phragmopedilum* rather than *Phragmopedium* suggested by Rolfe (1896) is mandatory today since the genus was published originally as *Phragmopedilum* by Pfitzer. In the same manner *Paphiopedilum* (rather than *Paphiopedium*

¹An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Henry Shaw School of Botany of Washington University.

²Ascherson, P. Flora d. Prov. Brandenburg, p. 700, *in nota*. 1864.

of Kerchove, 1894, or Rolfe, 1896) takes precedence. The regularity that Rolfe sought for the endings of the generic names within the group, and the change sought by Pfitzer on the basis of derivation are tempered by priority. The following keys to the genera, with necessary modification to generic names, are taken from Rolfe and Pfitzer in that order and are offered for comparison.

ROLFE'S KEY TO ORCHIDAEAE (ORCHIDACEAE OF PFITZER)

Suborder DIANDRAE (PLEONANDRAE of Pfitzer)

Tribe CYPRIPIDIEAE (CYPRIPEDILINAE of Pfitzer)

Ovary 3-celled with axile placentas; sepals valvate.

Leaves plicate; perianth persistent; seeds subglobose..... *Selenipedium* Rchb. f.

[3 species in South America and Brazil]

Leaves conduplicate; perianth deciduous; seeds fusiform..... *Phragmopedium* (Pfitz.) Rolfe

[11 tropical American species]

Ovary 1-celled with parietal placentas; seeds fusiform.

Leaves plicate; perianth persistent; sepals valvate..... *Cypripedium* L.

[about 30 widely scattered species in Europe, temperate Asia, and North America]

Leaves conduplicate; perianth deciduous; sepals imbricate..... *Paphiopedilum* Pfitz.

[46 species in tropical Asia]

PFITZER'S KEY TO ORCHIDACEAE

PLEONANDRAE

Tribe CYPRIPEDILINAE

A. VERNATION OF THE LEAVES CONVOLUTE, PERIGONIUM MARCESCENT, PERSISTING IN THE FRUIT.

a. Ovary trilocular, seed almost spherical with brittle outer coat..... *Selenipedium* Rchb. f.

Cypripedium L.

b. Ovary unilocular, seed elongate with fragile coat.....

a. Ovary trilocular, vernation of sepals valvate, margin of slipper-shaped labellum broadly involute or induplicate..... *Phragmopedium* (Pfitz.) Rolfeb. Ovary unilocular, vernation of sepals imbricate, margin of slipper-shaped labellum simple and straight, lightly incurved or recurved..... *Paphiopedilum* Pfitz.

Paphiopedilum callosum (Rchb. f.) Pfitz. and its var. *Sanderæ* Hort.—*Paphiopedilum callosum* was described as *Cypripedium callosum* by H. G. Reichenbach filius (1896). It was brought from Siam by Alexandre Regnier, of Paris, in 1885, and very little time elapsed between its importation and the possession of a plant by the Sander's Company of St. Albans in England. It was early recognized as a graceful and vigorous form and was soon in culture wherever there were orchid enthusiasts. (See pl. 31.)

The albino form, variety *Sanderæ*, appeared in culture in 1893 or 1894. Whether it flowered for the first time in England or France is a matter of debate; an anonymous article in the 'Journal of Horticulture' of 1912 says that it flowered for the first time in the autumn of 1893 in the collection of R. H. Measures, Esquire, at The Woodlands, Streatham. Be that as it may, in the Seventh Annual Show of the Royal Horticultural Society at the Inner Temple Gardens of May 23–25, 1894, it won a First Class Certificate when exhibited by Messrs. Sander and Sons of St. Albans. Both the Sander's plant and that of Measures appear to have come from the same source.

For several years the variety *Sanderæ* remained something of a rarity but came at length to be well represented in collections everywhere; its similarity to the

1949]

albino form of *Lawrenceanum* was commented upon but it was considered by most to be more graceful.

Paphiopedilum Lawrenceanum (Rchb. f.) Pfitz. and its var. *Hyeanum* (Rchb. f.)—*Paphiopedilum Lawrenceanum* (see pl. 31) was described as *Cypripedium Lawrenceanum* by H. G. Reichenbach filius in 1878. The plant was found on the bank of the Lawas River by Mr. F. W. Burbidge while on a collecting trip in North Borneo in the service of the Veitch Company. In December, 1878, it was brought to flower in the Veitch greenhouses. Dr. Reichenbach named it for Sir Trevor Lawrence, Baronet, M. P., a contemporary orchid enthusiast whose collection is described as "being of exceptional richness and beauty" (Reichenbach, 1878).

The albino form appeared spontaneously in the Linden cultures of ordinary *Lawrenceanum* which had been imported by Messrs. Lowe & Co. of Clapton. Mr. Jules Hye of Ghent, a fancier, was most eager to secure such a rarity for his own collection, and apparently Mr. Linden, after having sold it to him, decided to name the plant for his customer. It was shown in the April 27, 1886, meeting of the Royal Horticultural Society by two exhibitors, the Compagnie Continental, and R. B. White, Esquire, of Earlsfield, Surrey.

The new form was at first called *Cypripedium Hyeanum*, by various authors, but it was Reichenbach who first regarded it as a variety.¹ His description appeared in 'Lindenia,' of 1885, changing the nomenclature from *Cypripedium Hyeanum* (L.) Lind. & Rod. to *Cypripedium Lawrenceanum* Rchb. f. var. *Hyeanum* Rchb. f.

× *Paphiopedilum Maudiae* Hort.—The hybrid is a cross between *P. callosum* var. *Sanderae* and *P. Lawrenceanum* var. *Hyeanum*, with the latter as the seed parent (Wilson, 1923). It flowered for the first time in the early fall of 1900 in the houses of Messrs. Charlesworth & Co. of Heaton, Bradford, England, and on September 27 of that year took a First Class Certificate at the Manchester Orchid Society exhibition. A similar award was given when it was shown by Mr. G. W. Law-Schofield at the Royal Horticultural Society on July 30, 1901. Since that time it has been highly prized as a show plant, decorative plant, and commercial orchid. (See pl. 31).

Just who is to be credited with making the cross is a matter of conjecture. It has been reported that it was made in the Charlesworth establishment and again as having been made by two amateur growers, Major Mason and Mr. Charles Winn. In any event, the pot containing the seeds came into the possession of the Charles-

¹Reichenbach (Gard. Chron. 18:748) states: "Mr. Jules Hye Leysen, of Gand, Coupure 8, was so very kind as to send me the only flower we Europeans have had the opportunity of seeing . . . I immediately thought it might be an albino of Sir Trevor Lawrence's *Cypripedium* . . . I am persuaded we must regard it as *Cypripedium Lawrenceanum* variety *Hyeanum*, the name having been given, otherwise we might better call it 'Mons. Hye Leysen's individual' . . . The history is simply, that it was found at the old establishment at Linden amidst a mass of typical *C. Lawrenceanum*."

worth Company which is recorded as having produced the first flower. The plant was named for the daughter of Mr. Baguley, the Charlesworth foreman. The cross, of course, was inevitable since the parent forms were collector's items valued at more than 100 guineas a plant, a price which indicated the value then placed on such desirable forms.

There is a peculiarity in the nomenclature of the hybrid *Maudiae* which should be mentioned. If the specific, rather than the varietal, forms of the parent species had been crossed, the name *Maudiae* would have denoted a colored form. The albino form would then have to be designated by some such additional term as *albescens*. As it happened, \times *Paphiopedilum Maudiae* denotes the albino form, and the colored hybrid which appeared six years later had to be designated *P. Maudiae* var. *coloratum*.

From the albino form, several selections have been made. Among them are *P. Maudiae* var. *magnificum*, *P. Maudiae* WESTONBIRT variety, *P. Maudiae* DELL variety, and *P. Maudiae* BANK HOUSE variety.

The interspecific hybrid *Paphiopedilum Maudiae* exhibits hybrid vigor in both growth and flowering, for it is sturdier than either of its parents and flowers more frequently. There are certain striking characters in the hybrid which are readily seen in one parent or the other. The following table compares some of these characters in parents and offspring:

	<i>P. Lawrenceanum</i>	<i>P. callosum</i>	\times <i>Maudiae</i>
Leaves	Tessellated	Marbled	Tessellated
Petals	(a) Horizontal	Pendent or drooping	Intermediate (if otherwise it is closer to <i>callosum</i>)
	(b) Tip acute	Acuminate	Acute
	(c) Warted on upper and lower edges	Warted on upper edge only	Warted on upper edge only
Sepals	(a) Warted at base (b) Somewhat ciliate	Not warted at base Less ciliate	Not warted at base <i>As in callosum</i>

In order to clarify the positions of the species within the genus and the appearances of the entities involved, the following outline is added. The system is that of Pfitzer which is at present accepted but the only varieties mentioned are those bearing on this problem. All but the descriptions of *Maudiae* are from Sander's Orchid Guide of 1927.

Genus *Paphiopedilum*

Subgenus: OTOPEDILUM. (There are 3 subgenera. The others are BRACHYPETALUM and ANATOPEDILUM)

Section: PHACOPETALUM. (There are 11 sections of subgenus OTOPEDILUM)

Species: 1. <i>P. Curtisii</i>	6. <i>P. callosum</i>
2. <i>P. ciliolare</i>	<i>P. callosum</i> var. <i>Sanderae</i>
3. <i>P. superbiens</i>	7. <i>P. Lawrenceanum</i>
4. <i>P. Argus</i>	<i>P. Lawrenceanum</i> var. <i>Hyeanum</i>
5. <i>P. barbatum</i>	

P. callosum: Foliage marbled. Scape 1 to 2 feet, 1- or 2-flowered. Flowers large, variable, dorsal sepal white, shaded or green at base, striped and often flushed with dark crimson, petals pale green with rose-purple apices, warted and ciliated at upper margins, lip brown-purple. Winter to summer.

Var. *Sanderae*: Dorsal sepal white with apple-green stripes and radiating dorsal veins, petals pale green, whitish on the upper edges, lip pale green. Winter to summer.

P. Lawrenceanum: Foliage brightly tessellated. Scapes 1-2 feet high. Flowers large, bold, dorsal sepal white with purple-red stripes, greenish at base, petals horizontal, greenish with purple shading, chiefly at the tips and margins, black-warted on both edges. Lip dull purple tinted with brown, variable. Summer.

Var. *Hyeanum*: Dorsal sepal pure white with green stripes, petals yellowish green, lip greenish. Summer.

× *P. Maudiae* (Rolfe, 1900): An albino. Dorsal sepal very broad and rounded, white closely veined with bright green. Petals somewhat falcate, light green with darker veins and a few darker warts on the upper margins. Lip and scape light green. Flowering time various.

II. STATUS OF *Paphiopedilum Maudiae* AS A PARENT PLANT

The hybrid *P. Maudiae* combines the winter-flowering habit of one parent with the summer-flowering habit of the other and is one of a small group of albinos within its genus. It is, furthermore, an exceptionally beautiful plant. These features would seem to make it a highly desirable parent yet it has not been used to great extent perhaps because of its sterility. When *Maudiae* has been used in what would appear to be advantageous crosses there has been little seed produced and the extended flowering period characteristic of *Maudiae* has, as a rule, not been obtained in the offspring.

Albino-flowered forms are rare in *Paphiopedilum*, the great majority of species as yet not having produced any. Although there is a considerable number of advanced¹ albino hybrids today, they may be traced back to one or more of these basic forms (Black, 1933; Cooper, 1946).

1. *P. bellatum* var. *album* and *P. niveum* (subgenus BRACHYPETALUM). These are the only species in which true whites are formed. Even so *P. niveum* shows a faint peppering of purple when viewed closely.

2. *P. Lawrenceanum* (var. *Hyeanum*), *P. callosum* (var. *Sanderae*), and *P. Curtissii* (all in sect. PHACOPETALUM) have albino forms in which the white is striped and shaded with green. These belong to the "mottled group" characterized by marbled or tessellated foliage and petals ciliated and warted.

3. *P. Charlesworthii* var. *album* (sect. NEUROPETALUM) which may no longer be in cultivation.

¹In this study the expression primary hybrid is construed to mean species or variety hybrid. An advanced hybrid is one in which one or both parents is of hybrid origin.

4. *P. insigne* vars. *Sanderae* and *Sanderianum* (sect. NEUROPETALUM) is a soft yellow of variable depth according to the form. It is not striped, and white appears in the dorsal sepal. It is the chief member of the "insigne group."

Some success has been achieved by combining *Maudiae* with other albino varieties (Wilson, 1923):

HOLDENII (*Maudiae* \times *callosum* var. *Sanderae*).—Exhibited in 1909.

ALMA GAVAERT (*Maudiae* \times *Lawrenceanum* var. *Hyeanum*).—Flowered in 1911.

WARDEN (*Maudiae* \times *Holdenii*).—Flowered 1920.

EMERALD (*Maudiae* \times *Curtissii* var. *Sanderae*).—Exhibited in 1920.

ENCHANTRESS (*ALMA GAVAERT* \times *Curtissii* var. *Sanderae*).—Exhibited in 1921.

ROSETTII (*Maudiae* \times *insigne* var. *Sanderianum*).—Exhibited in 1908.

Before entering into a discussion of the crosses in which *P. Maudiae* and its parents have been involved, a further breakdown of the genus is necessary. The key given is taken from Pfitzer and may be used in conjunction with Charts I, II and III and their appendices:

KEY TO THE SUBGENERA OF PAPHIOPEDILUM

- A. Labellum a slipper, exauriculate (without ears or auricles), bag-shaped, having a very short claw at the fore of the narrow inwardly rolled margin; petals very broadly elliptical or almost orbicular; leaves shortly elliptical, tessellated above, more or less purple below, scape uniflorous.....Subgenus 1. **BRACHYPETALUM** Hallier¹
- B. Labellum a slipper, exauriculate, inclining downward, having a claw of almost equal length to that of the slipper on the front of the simple non-involute margin; petals elongate; leaves strap-shaped, green on both sides, scape several-flowered.....Subgenus 2. **ANATOPEDILUM** Pfitz.
- C. Labellum a slipper, auriculate, bag-shaped, having a claw almost as long as the slipper at the fore of the simple, non-involute margin; petals elongate; leaves varying, scape several or single-flowered.....Subgenus 3. **OTOPEDILUM** Pfitz.

KEY TO THE SECTIONS OF THE SUBGENUS ANATOPEDILUM

- A. Sepals striate between simple curving nerves; petals deflexed (bent outwardly), elongate with ciliate margins; staminode cylindrical, bent, the lower ascending part with long hair, the upper descending part glabrous above with two lobed apex.....Sect. **GONATOPEDILUM** Pfitz.
- B. Sepals striate between simple curving nerves; petals deflexed, elongate, twisted margins adorned with hairy warts; staminode directed upward and forward, arched over, pilose below the concave margin.....Sect. **CORYOPEDILUM** Pfitz.
- C. Sepals with extra striate curving nerves between tenuous reticulate nerves; petals curved, elongate, margin almost naked; staminode like that of the preceding section.....Sect. **PRENIPEDILUM** Pfitz.

KEY TO THE SECTIONS OF THE SUBGENUS OTOPEDILUM

- A. Staminode inversely heart-shaped, forked, enlarged on the back by a basal boss, acute, pilose. Leaves strap-shaped, uniform in tint, almost erect, green. Scape several-flowered, flowering simultaneously.
 - a. Petals narrow, hanging, often twisted on the lower margin, decorated with hairy warts, minutely spatulate at the apex. Leaves very narrow with hyaline margins.....Sect. **MYSTROPEDALUM** Pfitz.
 - b. Petals narrow from linear base toward the apex, frequently expanding into a blade, extremely divergent, nearly twisted, margin without warts. Leaves very narrowly yellow-margined.....Sect. **PARDALOPETALUM** Hallier

¹ *Brachypetalum* is not further divided to sections but is divided directly into species.

B. Staminode lightly forked, almost with an undivided boss at the back. Leaves broadly strap-shaped, recurved, uniform in tint, green or glaucous. Scape several-flowered, bracts emarginate, flowering successively..... Sect. COCHLOPETALUM Hallier

C. Staminode nearly orbicular, square, heart-shaped or almost heart-shaped. Sepals with tenuous reticulate nerves between simple curved nerves. Leaves green, uniform in tint, scapes unifloral, very rarely bifloral.

- Staminode nearly square, enlarged on the back by 3 low, slightly prominent bosses; petals spatulate..... Sect. STICTOPETALUM Hallier
- Staminode almost reverse heart-shaped, blunt, enlarged on the convex or plane back by one large central boss; petals more or less expanding into a blade toward the apex..... Sect. NEUROPETALUM Hallier
- Staminode heart-shaped, furrowed at the back, slightly bossed; petals elliptical..... Sect. THIOPETALUM Hallier
- Staminode almost round, split on the posterior with rolled-back lobes; petals oblong with wavy margins..... Sect. CYMATOPETALUM Hallier

D. Staminode half-moon-shaped, the fore part equally three-cusped; sepals with simple curving nerves uniting reticularly at the apex; petals strongly sigmoid, bent outwards at the apex, erect. Leaves green, uniform in tint, scape unifloral..... Sect. CERATOPETALUM Hallier

E. Staminode half-moon-shaped, with double horse-shoe-shaped or now and then nearly rhombic boss. Sepals net-veined or simply veined, petals clearly expanding into a blade toward the apex. Leaves more or less tessellate (checkered), scape unifloral..... Sect. SPATHOPETALUM Pfitz.

F. Staminode moon-shaped or semi-rounded, without a boss; sepals simply nerved; petals not expanding or hardly expanding into a blade toward the apex. Leaves clearly tessellate, scape unifloral, rarely bifloral.

- Petal margins naked or haired with equally disposed cilia..... Sect. BLEPHAROPETALUM Pfitz.
- Petal margins spotted or adorned with prominent warts provided with small brush-like hair tufts..... Sect. PHACOPETALUM Pfitz.

Maudiae has been crossed to members of nine of the eleven sections of the subgenus OTOPEDILUM or to individuals whose antecedents lie within these sections. (It has not been crossed to individuals belonging to sections PARDALOPETALUM or MYSTROPETALUM.) The section contributing the most germ plasm to individuals crossed with *Maudiae* appears to be NEUROPETALUM; PHACOPETALUM, the section from which *Maudiae* stems, and CYMATOPETALUM contribute somewhat less. Individuals emanating from the NEUROPETALUM group were used freely, probably in efforts to combine *Maudiae*'s everblooming character with some of the desirable "insigne" characters. Only one cross has been recorded with a BRACHYPETALUM species (*niveum*) and one with ANATOPEDILUM (*Rotbschildianum* in sect. GONATOPEDILUM). Of the 35 crosses in which *Maudiae* has been used (Sander's List, 1946), 11 have been with species, 3 with primary hybrids, and 21 with advanced hybrids. (See Chart I).

Paphiopedilum callosum has been crossed to members of nine out of the eleven sections of the subgenus OTOPEDILUM, or individuals having their antecedents therein. (It has not been crossed to individuals with a background in MYSTROPETALUM or PARDALOPETALUM). PHACOPETALUM, to which *callosum* and *Lawrenceanum* belong, is the section contributing the greatest number of individuals to these crosses with NEUROPETALUM and others contributing lesser numbers. It has been crossed to all of the species within the subgenus BRACHYPETALUM and with sections CORYOPEDILUM and PRENIOPEDILUM of the subgenus ANATOPEDILUM.

Of its 55 crosses, 29 have been with species, 13 with primary hybrids, and 13 with advanced hybrids. (See Chart II and Appendix).

Paphiopedilum Lawrenceanum has been crossed to representatives of all of the eleven sections of *OTOPEDILUM*. Again, *PHACOPETALUM* and *NEUROPETALUM* contribute the most germ plasm to the individuals used in these crosses, with other sections contributing lesser amounts. It has been crossed with all the *BRACHYPETALUM* species and with individuals belonging to two of the sections of the subgenus *ANATOPEDILUM* (*Gonatopedilum* and *Coryopedilum*). Of the 62 crosses in which *Lawrenceanum* has been involved, 30 have been with species, 17 with primary hybrids, 15 with advanced hybrids. (See Chart III and Appendix).

The only reasonably complete list of orchid hybrids available is Sander's 'Complete List of Orchid Hybrids' (1946). This lists *Maudiae* as having been used in 35 crosses, *Lawrenceanum* in 62, and *callosum* in 55. Of the 35 offspring of *Maudiae* only 7 have been used to produce 41 named offspring of their own. Twenty *Lawrenceanum* offspring have been used in 123 crosses, and 15 *callosum* offspring in 74, with *Maudiae* being the most productive offspring in either case. It must be remembered, however, that Sander's List does not necessarily present a true picture of sterility or fertility. It simply lists the crosses giving rise to named and registered varieties and gives no account whatever of the crosses made wherein the grower considered the result not worth saving. It is thought, however, that most of the early crosses were named and registered since even the poor ones were regarded as having botanical interest.

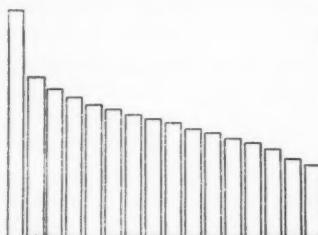
That both *Lawrenceanum* and *callosum* were crossed to more species than *Maudiae* is to be expected since they are older and have been known to horticulturists for a much longer time. It is reasonable to assume from the record that both of these species cross freely with other members of the genus. *Maudiae* appears to be slightly restricted, in comparison to its parents, in the number of sections to which it has been crossed. In part, this restriction may simply be a reflection of the horticulturist's discrimination; crosses made with *callosum* and *Lawrenceanum* that had proved inferior were probably not repeated with *Maudiae*. Also it is to be noted that many of the individuals to which *Maudiae* has been crossed have been advanced hybrids, and this has probably contributed to a lack of seed set. At any rate, hybridizers have not been able to obtain sufficient seed when using *Maudiae* as a parent to combine its undoubted qualities with those of other parents; large numbers of crosses must be made to obtain a small amount of seed.

III. ANALYSIS OF ROOT-TIPS

An attempt was made to analyze the chromosome complements of *P. callosum*, *P. Lawrenceanum* (the albino forms were not available), and several forms of \times *Maudiae*. For this purpose root-tip smears were used. It was felt that in addition to observation with the microscope and scrutiny of camera-lucida drawings the construction of ideograms would be fruitful. The value of ideograms in this case will be discussed in a following paragraph.

Root-tips were killed and fixed, after quartering, in a solution containing six parts of absolute alcohol to three parts of chloroform to one part of glacial acetic acid. It was necessary to leave the tips in the killing and fixing fluid for at least fifteen minutes although they were often, for reasons of necessity, allowed to remain at least an hour. Tips that could not be squashed and stained immediately after removal from the killing and fixing fluid were kept in an aqueous solution of 45 per cent glacial acetic acid.

The first smears were made from tips of *P. callosum*. Aceto-orcein as well as aceto-lacmoid was used as a stain. After completing observations on *P. callosum* aceto-lacmoid only was used in studying *P. Lawrenceanum* and *P. Maudiae*. The squash procedure used was that outlined by Mehlquist (1947). It was found later in the investigation that the Feulgen technique outlined by Meyer (1943) gave excellent results generally but that for studies involving the centromere region aceto-lacmoid was the best agent when used on root tips that had not been in the Carnoy's fluid for more than fifteen minutes.



Text-fig. 1. *P. callosum*. Comparative length of chromosomes.



Text-fig. 2. *P. Lawrenceanum*. Comparative length of chromosomes.

The construction of ideograms was based upon camera-lucida drawings of mid-metaphase cells so flattened that all parts of a chromosome were in one plane. Ten such plates were obtained for *P. callosum* but only four could be found for *Lawrenceanum* and five for *P. Maudiae*. It was the original plan to study ten of each, but, although many root-tips were examined, only this small number was found fit for use. Indeed, it was often difficult to obtain tips showing any divisions at all. On the basis of such small numbers the ideograms are presented here only as indicators and not as final pictures of chromosome complements. Haploid ideograms of *P. callosum* and *P. Lawrenceanum* based upon excellently flattened anaphase cells clearly indicating centromere position are presented. These were not used in the preparation of the final ideograms showing length relationships.

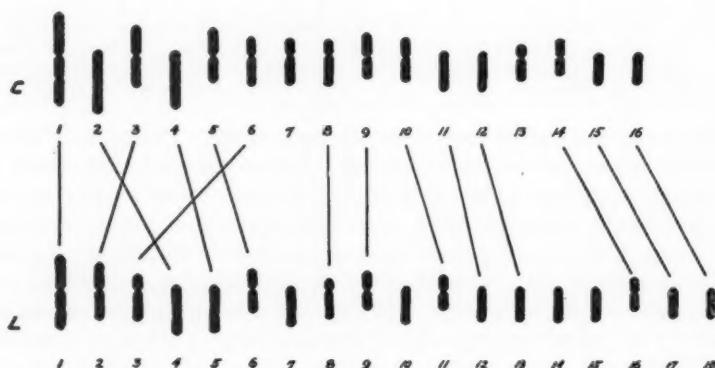
After preparation of camera-lucida drawings, the chromosomes were paired according to length, position of centromere, and placement of secondary constrictions. The basic ideogram thus consisted of the diploid number. For the final ideogram the lengths of the two members of a pair were averaged and the averages of all corresponding pairs were in turn averaged. The final ideogram therefore

shows the haploid number. The haploid ideograms of *P. callosum* and *P. Lawrenceanum* are fundamentally alike. Both show a noticeably long chromosome number 1. The difference in length between chromosomes 1 and 2 is less in *P. Lawrenceanum* than in the other. Aside from chromosome 1 all chromosomes show a very close intergradation in size. (See text-figs. 1 and 2.)

Chromosome counts in various "horticultural Cypripediums," including *P. callosum*, *P. Lawrenceanum*, and the interspecific hybrid *Maudiae*, have been made by Mehlquist (1947a), Duncan (1945, 1947), and others. Some of these counts were verified during this investigation: *P. callosum* has a diploid number of 32; *P. Lawrenceanum*, 36; \times *Maudiae*, 34 (see pl. 32); *P. barbatum*, 38; *P. Curtissii*, 36; and *P. superbiens*, 38.

Paphiopedilum callosum, with a $2n$ number of 32, was analyzed first and ideograms were prepared. All but a few of the sixteen pairs of chromosomes have no identifying morphological features and exhibit a subtle intergradation in lengths. The following chromosomes are best recognized at sight:

1. The longest pair has median centromeres; the secondary constriction is about midway on one arm.
2. A pair intermediate in length often appears to be composed of three pieces of chromatin to each individual. An end piece is a satellite.
3. One pair, longer than average, each with one ball type end, appears to have subterminal centromeres.



Text-fig. 3. Diagrammatic representation of the chromosomes of *P. Lawrenceanum* (L) and *P. callosum* (c), based on anaphases in root-tips which clearly disclosed the position of the centromeres. Chromosomes arranged according to length. The numbers are merely for convenience and do not signify that chromosomes having the same numbers are alike. The lines connecting c and L chromosomes suggest possible homologues.

The second secondary constriction is on a chromosome of intermediate length with subterminal centromere in one species and on a chromosome with interstitial centromere in the other. The constriction is not shown because the positions of these chromosomes are uncertain.

4. One, or possibly two, pairs shorter than the average, with one ball type end, appears to have subterminal centromeres.

The remaining chromosomes are so alike morphologically and vary so little in length that they cannot be identified as individuals upon observation. However, it can be shown that within the *callosum* complement there are six terminal or subterminal pairs and ten pairs in which the centromeres are interstitial. (See text-fig. 3.)

The chromosomes of *P. Lawrenceanum*, by virtue of their similarity, remain as cryptic as those of *P. callosum*. Here the longest pair is readily identified by having a median, or close to median, centromere and is seen to possess a secondary constriction. Even the smallest chromosomes of *Lawrenceanum* cannot be distinguished readily because of their great similarity in length to the next smallest pair. Thus, aside from the longest pair, the remaining seventeen pairs verge closely on one another in size. The difference in the chromosome numbers of *P. callosum* and *P. Lawrenceanum* appears to be in an increase of small chromosomes in the complement of *P. Lawrenceanum*. It can be shown that in *P. Lawrenceanum* there are ten pairs of terminal or subterminal chromosomes and eight pairs in which the centromeres are interstitial. (See text-fig. 3.)

The chromosomes of the interspecific hybrid *Maudiae* presented the same morphological anonymity as those of the parental forms. Again the long pair with median centromere and clearly defined secondary constriction was readily noted. There are two pairs longer than the average with centromeres between the median and subterminal points, and two pairs of average length with median centromeres but these are not often readily discernible.

The satellites pair of intermediate length seen in *callosum* was seen in *Maudiae* and presented an interesting situation. In regard to this chromosome, *Maudiae* var. *magnificum* is visibly an inversion heterozygote. A cell was found in which it was apparent that half of one of the chromosomes of this pair is inverted. The inverted half bears the centromere, and since the centromere is subterminal in one, it becomes interstitial in the other.

The $2n$ chromosome configuration of *Maudiae* should consist of 10 chromosomes with terminal or subterminal centromeres and 8 with interstitial centromeres from the *Lawrenceanum* parent, while of the 16 chromosomes contributed by *callosum* 6 should be terminal or subterminal and 10 would be interstitial. Attempts to construct an ideogram showing the diploid number were not rewarding. It may be assumed from these attempts, however, that the close intergradation of chromosome lengths which characterize the parents is characteristic of the offspring.

The value of the ideograms in the analysis of these chromosome complements would appear to be at best only moderate. Ideograms can be used only as approximations for various reasons:

1. The lengths of members of a chromosome pair are not always equal; the longest chromosomes in the basic ideograms, for example, rarely agree exactly in

length. This may be a result of a squashing which leads to distortion not only in length but in other dimensions.

2. Lengths of chromosomes vary from metaphase to metaphase.
3. The length ratio of one pair to another may vary from one metaphase to another because of pressure applied in squashing.
4. The order of 16, 17 or 18 pairs in an ideogram must undoubtedly differ to some degree when there are many of approximately the same lengths lacking distinct morphological features and have been, in addition, subjected to pressure.
5. Centromeres may vary in size or become so small as to be apparently lacking.
6. Satellites vary in size as do also the portions of a multi-piece chromosome.
7. A chromosome may break under pressure not only at the centromere but at other regions. Thus a chromosome could appear to have a median centromere when it is actually of the subterminal type, or a median type, when broken in two, appear to be two subterminal chromosomes.

Despite these reasons for not placing too much faith in the ideogram as an actual picture of the chromosome complement there was sufficient resemblance among the basic ideograms to predict with considerable accuracy the appearance of the final ideogram.

Ideograms of the haploid numbers of various *Paphiopedilum* species published to date by Duncan and MacLeod (1948a, 1948b) include representatives of subgenera BRACHYPETALUM and ANATOPEDILUM and of the sections of OTOPEDILUM except SPATHOPETALUM, BLEPHAROPETALUM and PHACOPETALUM. These, for the most part, indicate a chromosome number 1 recognizable by its length and possessing a median or near median centromere. Chromosome number 2 may approximate or nearly approximate it in length but there is usually a difference. From chromosome number 2 on there is a close intergradation in length down to the smallest chromosome. In this they agree with ideograms published earlier by Francini (1931, 1932, 1934). Among the intermediate chromosomes there is one with a secondary constriction. These same generalities are true for the chromosomes of *P. callosum*, *P. Lawrenceanum*, and *P. Maudiae*, except that these three appear to have an additional secondary constriction on chromosome number 1. Only one species, *P. exul*, ideogrammed by Duncan and MacLeod, shows a secondary constriction on number 1 and none on any other chromosome. (Two species ideogrammed by Duncan and MacLeod exhibit a secondary constriction on number 2 and on no other chromosomes. These are *P. Druryi* and *P. Spicerianum*.)

The following list presents the $2n$ chromosome numbers to date of species within the genus:

CHROMOSOME NUMBERS OF SPECIES OF PAPHIOPEDILUM

	Chromosome Numbers	Authority*	Date
Subgenus BRACHYPETALUM Hallier			
<i>P. bellatum</i> (Reichb. f.) Pfitz.	26 26	D GM	'47 '47
<i>P. concolor</i> (Batem.) Pfitz.	26	D&ML	'48
<i>P. niveum</i> (Reichb. f.) Pfitz.	26 26	GM D	'47 '47
<i>P. Delanatii</i> Guill.	26 26	D GM	'47 '47
Subgenus ANATOPEDILUM Pfitz.			
Sect. GONATOPEDILUM Pfitz. <i>P. Rothschildianum</i> (Reichb. f.) Pfitz.	26, 28 26	D D&ML	'47 '49
Sect. CORYOPEDILUM Pfitz. <i>P. praestans</i> (Reichb. f.) Pfitz.	28 28	D D&ML	'47 '49
<i>P. philippinense</i> (Reichb. f.) Pfitz.	26	D&ML	'49
Sect. PRENIPEDILUM Pfitz. <i>P. Stonei</i> (Hook. f.) Pfitz.	26 26	D D&ML	'47 '49
MARY REGINAЕ Hort.			
Subgenus OTOPEDILUM Pfitz.			
Sect. MYSTROPETALUM Pfitz. <i>P. Parisii</i> (Reichb. f.) Pfitz.	26 26	D D&ML	'47 '49
Sect. PARDALOPETALUM Hallier <i>P. Lowii</i> (Lindl.) Pfitz.	26 26	D D&ML	'47 '49
<i>P. Haynaldianum</i> (Reichb. f.) Pfitz.	26 26	D D&ML	'47 '49
Sect. COCHLOPETALUM Hallier <i>P. Chamberlainianum</i> (O'Brien) Pfitz.	26	D	'47
<i>P. glaucophyllum</i> J. J. Smith	36	D	'47
Sect. STICTOPETALUM Hallier <i>P. birsutissimum</i> (Lindl.) Pfitz.	26	D&ML	'49
Sect. NEUROPETALUM Hallier <i>P. villosum</i> (Lindl.) Pfitz.	26 28 26 26	F F GM D D&ML	'34 '31 '47 '47 '48
<i>P. Boxallii</i> (Reichb. f.) Pfitz.	26 26	GM D&ML	'47 '48

* The abbreviations used for authorities are: D, Robert E. Duncan; D&ML, Robert E. Duncan and Raymond A. MacLeod; F, Eleanora Francini; GM, Gustav A. L. Mehlquist.

	Chromosome Numbers	Authority*	Date
<i>P. insigne</i> (Wall.) Pfitz.	32 26 26 26	F GM D D&ML	'31 '47 '47 '48
<i>P. exul</i> (O'Brien) Pfitz.	26 26	D D&ML	'47 '49
<i>P. Charlesworthii</i> (Rolfe) Pfitz.	26 26	D D&ML	'47 '49
<i>P. Gratrixianum</i> Rolfe	26 26	D D&ML	'47 '48
Sect. THIOPETALUM Hallier			
<i>P. Druryi</i> (Bedd.) Pfitz.	26 26	D D&ML	'47 '49
Sect. CYMATOPETALUM Hallier			
<i>P. Spicerianum</i> Pfitz.	30 28 28, 30	F D D&ML	'31 '47 '49
Sect. CERATOPETALUM Hallier			
<i>P. Fairrianum</i> (Lindl.) Pfitz.	26 26 26	D GM D&ML	'47 '47 '49
Sect. SPATHOPETALUM Pfitz.			
<i>P. venustum</i> (Wall.) Pfitz.	36 42	F D	'31 '47
Sect. BLEPHAROPETALUM Pfitz.			
<i>P. tonsum</i> (Reichb. f.) Pfitz.	34	D	'47
<i>P. Mastersianum</i> (Reichb. f.) Pfitz.	32	D	'47
<i>P. javanicum</i> (Reinw.) Pfitz.	36	D	'47
<i>P. Dayanum</i> (Reichb. f.) Pfitz.	34	D	'47
<i>P. Wardii</i> Summerhayes	40-45	D	'45
Sect. PHACOPETALUM Pfitz.			
<i>P. Curtisii</i> (Reichb. f.) Pfitz.	36 36	D GM	'47 '47
<i>P. superbiens</i> (Reichb. f.) Pfitz.	38	D	'47
<i>P. barbatum</i> (Lindl.) Pfitz.	32 38 38 38	F F D GM	'31 '34 '47 '47
<i>P. callosum</i> (Reichb. f.) Pfitz.	32 32	D GM	'47 '47
<i>P. Lawrenceanum</i> (Reichb. f.) Pfitz.	36 36	D GM	'47 '47

1949]

IV. MEIOSIS

Aceto-lacmoid and aceto-orcein gave metaphase I smear preparations which were clear enough to determine the nature of pairing but the outlines of the chromosomes were often not sharply defined. A modification of the Feulgen technique, although somewhat better, gave much the same result. These methods also proved unsatisfactory for a study of the prophase chromosomes; all of these methods seemed reasonably good for material in anaphase I or later stages. The difficulty was not remedied even when an iron aceto-carmine mordant was added to the Carnoy's Fluid used for killing and fixing. The situation was further complicated by restrictions on the number of buds available; forty were used in the course of the study of pollen mother cells. It must be remembered that none of the plants involved are frequent bloomers, the parental forms blooming once yearly and *Maudiae* at most twice.

It was found after considerable experimentation that the best preparations were obtained by making permanent slides. Anthers were dropped in Carnoy's Fluid for 10-15 seconds and then put in CRAF for 24 to 48 hours. They were then washed and run through the usual tertiary butyl alcohol series and, after infiltration, were embedded. Sections were cut at 10 μ and then stained in crystal violet and safranin (Stockwell, 1934). This method gave results in pachytene and early diplo-tene which could not be obtained with the smear methods mentioned above, and the metaphase chromosomes were sharply outlined. A peculiarity in the staining effect was noted with the use of crystal violet and safranin. When the slides were left in the stain for a long time both meiotic and mitotic chromosomes were stained dark purple. When exposed to the stain for about 15 minutes the meiotic chromosomes were red while the mitotic nuclei or chromosomes were blue. At an exposure of about 12 minutes both meiotic and mitotic chromosomes were red.

No satisfactory study of chiasmata was made because of the extremely reduced size of the bivalents at mid-metaphase and because the procedure adopted does not spread the chromosomes sufficiently as the smear method so often does. Diakinesis, a stage favorable for the study of chiasmata in many other plants, could not be prepared suitably by any of the methods cited above.

P. Maudiae Hort. var. *magnificum* furnished most of the hybrid material studied although WESTONBIRT and DELL varieties were examined; the last do not appear to differ from *magnificum*.

PAPHIOPEDILUM CALLOSUM (2n = 32)

Prophase I.—Pairing appears to be normal when viewed in the pachytene stage.

Permanent preparations of diakinesis in *callosum* resemble those of *Maudiae* prepared by aceto-lacmoid smears or the Feulgen technique. Within the various techniques employed in this study it may be said that diakinesis in the two species and the hybrid is not a favorable stage for study. The chromosomes appear to be in a fluid or somewhat fluid state and are therefore poorly defined by the stain; large patches of chromatin are occasionally seen where the chromosomes appear to

have stuck together. This perhaps represents a time when the matrix is being elaborated most freely and is therefore quite thin in consistency. Some chiasmata can be seen but no accurate over-all picture can be given. Occasionally they appear as relatively colorless strands between the ill-defined chromosomes and again they appear to be surrounded with enough matrix to render them stainable. Among the chromosomes of intermediate length, two ring configurations have been noticed: one with no free ends and another in which one of the chiasmata is apparently not terminalized so that a short portion of one end of each chromosome is free. The same pair may be involved in both cases. Among the shortest chromosomes (at least those with subterminal centromeres) bivalents are formed with only one chiasma. The longest pair appears to form three or four chiasmata. The nucleolus is plainly visible at diakinesis.

Metaphase I.—Metaphase chromosomes have not been stained as clearly as desired by smear methods but were clear enough to determine pairing; chiasmata could not be properly interpreted. Twenty-five metaphase cells examined showed pairing to be in 16 bivalents. (See pl. 32).

Of 114 metaphase plates seen in side view, 107 appeared to have all their chromosomes in the plate in the normal fashion. One cell appeared to have one lagging chromosome, 2 were doubtful as to fragments or isolated chromosomes, and 5 appeared to have isolated chromosomes or fragments in each. It is entirely possible that these apparent abnormalities existed as a result of smearing.

Anaphase I.—Fifty-six anaphase cells were examined and no anaphase bridges were observed. One cell appeared to have a fragment between the two poles. Anaphase appears to be normal.

Telophase I.—No cell wall is formed at the close of division I. An interphase nucleus is formed.

Telophase II.—Five hundred tetrads were examined. No micro-grains or small extra cells were found within the thick wall.

Pollen grains.—Pollen grains were mounted in aceto-lacmoid for staining but were not pressed. The grains are elliptical to spherical in shape. Of 500 grains examined only 8 were found to be empty; no shrunken or distorted grains were found. The grains are slightly smaller than those of *P. Maudiae*. (See section on pollen grains, \times *Paphiopedilum Maudiae*).

PAPHIOPEDILUM LAWRENCEANUM ($2n = 36$)

Prophase I.—No leptotene or zygotene nuclei have been studied but pachytene and early diplotene nuclei have been observed. The crystal violet-safranin technique was used. Pairing as observed in pachytene appears to be regular throughout and no abnormalities were noticed. The early diplotene stages examined show the initial repulsion between the paired chromosomes.

Metaphase I.—Only 2 metaphase I cells suitable for study were found. These indicated pairing to be in 18 bivalents.

Anaphase I.—Observations on a large number of these cells indicate no apparent abnormalities. Bridges are not formed nor do there appear to be any lagging chromosomes or fragments in evidence. The chromosomes do not appear to be split in readiness for division 2 at this stage.

Telophase I.—An interphase nucleus is formed at this stage but no cell wall is formed. Eighteen chromosomes were counted at one pole in an early telophase.

Metaphase II.—Examination of metaphase II cells indicated that division had been regular. The regularity with which 18 chromosomes are disposed to each pole serves as additional evidence that 18 bivalents are formed at metaphase. (See pl. 32).

Anaphase and Telophase II.—No abnormalities are evident and the tetrads formed resemble those of *P. callosum*. A tetrad was found in which 18 chromosomes could be counted at one pole.

Pollen grains.—Pollen grains are elliptical to spherical and about the same size as the *callosum* grains. Of the 500 grains examined, only 2 were found to be empty. (See section on pollen grains, \times *Paphiopedilum Maudiae*.)

\times PAPHIOPEDILUM MAUDIAE Hort. ($2n = 34$)

Prophase I.—In the pachytene of *P. Maudiae* the nucleolus appears as a well-defined almost colorless body in intimate contact with chromosomal material. Although in sectioning the knife may frequently remove the nucleolus from cells, it is visible nonetheless in many others. Its attachment to a chromosome is noticeable. It is impossible to tell which chromosome is involved since the pachytene nucleus represents a tangle of long slim threads whose ends, except in chromosomes cut through by the knife, are often not visible. As with *callosum* and *Lawrenceanum* two nucleoli are occasionally visible in the mitotic cells forming the jacket around the pollen mother cells but only one nucleolus has been seen in the PMC's. The nucleoli seen in the PMC's are larger than those seen in mitotic cells.

There have been observed in the pachytene and pachytene-early diplotene chromosome configurations which suggest inversion and deletion but the chromosomes are so attenuate and the suspected loops or buckles so small that it has been impossible to ascertain this. The presence of inversion loops in pairing is to be expected in view of the presence of anaphase bridges.

As in *Lawrenceanum* the beadlike effect of the chromomeres is evident at this stage.

Metaphase I.—The staining with smear methods was suitable enough to examine pairing. Of the 27 metaphase cells of *P. Maudiae* examined, 26 showed 17 bivalent chromosomes. (See pl. 34). One cell showed 16 bivalents and 2 univalents. It appears that two of the *Lawrenceanum* chromosomes are pairing.

Anaphase I.—A total of 483 anaphase I cells were examined and several abnormalities were found:

a. Cells with 1 bridge but no fragments.....	17
b. Cells with 2 bridges but no fragments.....	1
c. Cells with 1 bridge and 1 fragment.....	13
d. Cells with 1 bridge and 2 fragments.....	1
e. Cells with 2 bridges and 1 fragment.....	2
f. Cells with 1 fragment (or small isolated chromosome).....	15
TOTAL	49

Of the cells examined 10.1 per cent showed abnormalities.

A further analysis of anaphase I was made possible through the observation of 4 cells in which the chromosomes could be counted at one or both poles. While this number is far too small to be regarded as significant the information is included to amplify the notes above.

1. Two cells showed clearly 17 chromosomes at one pole but a count could not be made at the other pole. There were no lagging chromosomes in evidence. The chromosomes were split in readiness for division 2 but this partial separation may have been caused by smearing.

2. One cell showed 17 chromosomes at one pole and 16 at the other. One chromosome lagged but appeared to be slightly closer to the pole with 17. Again the chromosomes were split.

3. One cell had 17 chromosomes at each pole; these were split for division 2.

Tetrads.—Examination of 527 tetrads was made. The arrangement is primarily that of 2 cells in each of two planes although 4 in one plane is not rare. The presence of a micro-grain or micro-cell, a small, extra cell within the tetrad wall, was occasionally noted.

<i>Apparently normal groups:</i>	
1. Two cells in each of two planes.....	417
2. Four cells in one plane.....	72

<i>Apparently abnormal groups:</i>	
1. Two cells in two planes plus one micro-grain.....	28
2. Four cells in one plane plus one micro-grain.....	4
3. Two cells in one plane (diad) plus one micro-grain.....	1
4. Three cells in one plane (triad) plus one micro-grain.....	5
TOTAL	527

Of tetrads examined 7.2 per cent showed irregularities.

Pollen.—In general the pollen grains range from elliptical to spherical. Of 500 grains examined 54 (10.8 per cent) were empty and some of them were distorted. (See pl. 33). Four of the empty grains were about one-third the normal size. The full regular cells are slightly larger than those of *P. callosum* and *P. Lawrenceanum*.

Measurements of 100 *Maudiae* pollen grains and 100 each of *callosum* and *Lawrenceanum* indicated that those of *Maudiae* average .0580 mm. along the long axis, while those of *callosum* and *Lawrenceanum* are .0530 and .0526 respectively. That the slight difference in size between the grains of the offspring and the parents is not merely based on variation within the samples was confirmed with a standard deviation test.

1949]

In both species and in the hybrid, leptotene and zygotene probably occur when the bud is quite small. Just how soon pachytene begins is not known but apparently pachytene and pachytene-early diplotene go on for considerable time, sometimes even a matter of days, depending upon environmental conditions. The remaining stages, particularly diakinesis and metaphase I, progress rapidly.

The lengths of some buds, divested of enfolding bracts, are listed together with the meiotic stages exhibited:

P. callosum

13.0 mm.	Pachytene
15.0 mm.	Pachytene
16.5 mm.	{ Pachytene to diakinesis Early metaphase I Metaphase I
17.0 mm.	Primarily diads. A few metaphase and anaphase I cells
18.0 mm.	Tetrad

P. Lawrenceanum

16.5 mm.	Pachytene, early diplotene
18.0 mm.	{ A few metaphase and anaphase I cells but chiefly division 2 Division 2 Tetrad
18.5 mm.	Division 2
19.0 mm.	Pollen grains

× *P. Maudiae*

13.0 mm.	Pachytene
15.5 mm.	Pachytene
16.5 mm.	Diakinesis to early metaphase I
17.0 mm.	{ Pachytene Pachytene to diakinesis Pachytene to mid-metaphase I
18.0 mm.	1. Metaphase I 2. Telephase I through division 2
18.5 mm.	Tetrad

V. DISCUSSION

It will be noticed in the anaphase I data of the hybrid that of the 49 cells listed as showing disorders, group *c* (13 cells) is characterized by one bridge and one fragment. This is the typical result of pairing between two chromosomes when one of them has an inversion not involving the centromere and a crossover occurs within the inverted region.

Group *a* (17 cells) exhibits the bridge but no fragment. Two possibilities exist here: either the fragment was not visible or it did not exist. Since none of the fragments observed either with or without bridges were large it is possible that in these cases it had been displaced by smearing or that it had been concealed by

the chromosomes at one or the other of the poles. There being evidence that inversions exist, this possibility must be given the more credence. The other possibility is that in these cells no fragment existed as a result of an inversion bridge. This would necessitate another hypothesis for the origin of a bridge without a fragment, and there is no evidence here to support such a hypothesis. The single cell in group *b* with two bridges but no fragments should be considered in the same light except that in this group two chromosome pairs were probably involved.

Group *e* (2 cells) is characterized by two bridges and one fragment. The most logical assumption here is that one of the fragments was rendered invisible as in the case above. The single instance of one bridge and two fragments (*d*) may well indicate the breakage of one bridge before the other. In these cases, as in *b*, two chromosome pairs would be involved.

Group *f* is composed of 15 cells which showed one fragment or small isolated chromosome. It is thought that these were true fragments since they were quite small. In such a case the bridge would have been already broken. However, the possibility that these might have been lagging chromosomes cannot be overlooked since many of the typical mid-metaphase I bivalents of the hybrid are small.

An interesting case is presented by the pair of chromosomes of intermediate length with prominent secondary constriction. It is this pair which exhibits the inversion mentioned in the section on root-tip analysis. (See pl. 32). Half of the chromosome is involved in the inversion for which the hybrid examined is heterozygous, and the inversion, when viewed under the microscope, appears to be terminal. The possibility must not be overlooked that there is chromatin material here which cannot be seen and would render the inversion interstitial. It has long been felt that inversions generally did not involve chromosome ends (Darlington, 1937; Kossikov & Muller, 1935; Muller, 1938). However, there is considerable evidence to date that terminal inversions do occur (Kauffmann, 1937; Sutton, 1940; Carson, 1944; Carson & Stalker, 1947), and the possibility that the inversion mentioned here is truly terminal must not be brushed aside. This inversion, since it involves the centromere, would not bring about the formation of a bridge. A single crossover within the inversion would result in a duplication-deficiency chromatid as well as one complete chromatid going to each pole. Of the complete chromatids, one would show the inversion (Sturtevant & Beadle, 1939).

It will be noticed that although 10.1 per cent of the anaphase I cells exhibited disorders, only 7.2 per cent of the hybrid tetrads were visibly abnormal. This probably can be taken to mean that some of the tetrads, although appearing normal, are not so. It cannot be said that there is any absolute correlation between the 10.8 per cent visibly non-viable pollen and the similar percentage of visible anaphase I abnormalities even though it is suggestive. No doubt there are other factors to be considered. The 10.8 per cent of non-staining pollen grains is not a true estimate of the hybrid's sterility in view of growers' experiences in attempting to use *Maudiae* as a parent plant. There are, no doubt, many pollen grains which appear quite normal but whose viability is terminated at later stages. Male gametes

may become non-viable in the pollen tube; the pollen tube may grow too slowly; the egg may be non-viable; the zygote may be non-viable; or the seedling perish early in its existence.

That the 10.8 per cent non-viable pollen is not a complete picture of the sterility of the hybrid is supported by what is known of pairing in *Maudiae*. It will be remembered that pairing in *Maudiae* was typically indicated by 17 bivalents at metaphase I. This suggests pairing between two *Lawrenceanum* chromosomes, and if two chromosomes are like enough to pair consistently this would in turn suggest polyploidy. It is entirely reasonable to assume that such pairing is the result of polyploidy. A glance at the list of chromosome numbers at the close of section III reveals that throughout subgenera *BRACHYPETALUM* and *ANATOPEDILUM* the *n* number is 13. In the subgenus *OTOPEDILUM*, the group to which all of the individuals dealt with in this study belong, higher *n* numbers approach the triploid level. It is suggested that this increase in chromosome number is the result of hybridization between groups that cannot be named at this time for lack of evidence.

The mere statement that pairing in *Maudiae* is in 17 bivalents and that the 2 remaining *Lawrenceanum* chromosomes pair is probably an over-simplification. *P. callosum* is characterized, as we have seen, by a chromosome set of 6 pairs of terminal or subterminal chromosomes and 10 interstitial pairs while *P. Lawrenceanum* possesses 10 terminal or subterminal pairs and 8 interstitial pairs. The difficulties of pairing a *Lawrenceanum* and a *callosum* chromosome for each of 16 bivalents (in addition to the bivalent already formed by each of two *Lawrenceanum* chromosomes), in view of the differences in morphology, are apparent. It is highly probable that some *callosum* chromosomes are pairing amongst themselves as well as with *Lawrenceanum* chromosomes, and this possibility would exist equally well for chromosomes of *Lawrenceanum*. Under such conditions gametes could be produced which would lack necessary genic elements. From the foregoing facts it seems logical to conclude that the causes of sterility in the hybrid are:

1. Visible disorders in anaphase I due to inversions.
2. Invisible disorders at anaphase I due to an inversion which includes the centromere and therefore results in duplication-deficiencies.
3. Pairing of some *callosum* chromosomes and some of the *Lawrenceanum* chromosomes among themselves (because of their polyploid background) takes place so that some of the gametes are without necessary chromatin material.

VI. SUMMARY

1. A cytological study was made of the \times *Paphiopedilum Maudiae* Hort., the result of a cross between the albino forms of *P. callosum* and *P. Lawrenceanum*. Because of its high sterility, *P. Maudiae* as a parent plant has rarely, if ever, produced any offspring of a quality equal to, or exceeding, its own.

2. A short discussion of the genus and the histories of the parental forms and the offspring are set forth.

3. Some observations are made on the status of \times *Paphiopedilum Maudiae* Hort. as a parent plant.
4. A cytological analysis of root-tips of the parental forms and the hybrid gave the following results:
 - a. Chromosome numbers of *P. callosum*, *P. Lawrenceanum*, and *P. Maudiae* are confirmed as being 32, 36, and 34, respectively. Two other species counts were also confirmed (*P. barbatum*, 38; *P. Curtissii*, 36; *P. superbiens*, 38).
 - b. *P. callosum* has 6 pairs of chromosomes with terminal or subterminal centromeres and 10 pairs with interstitial centromeres.
 - c. *P. Lawrenceanum* has 8 pairs with interstitial centromeres and 10 with terminal or subterminal centromeres.
 - d. *P. Maudiae* is heterozygous for an inversion which seems to be terminal.
5. Study of meiosis in the parental forms and the hybrid gave the following results:
 - a. *P. callosum* and *P. Lawrenceanum* undergo normal meioses with bivalent pairing.
 - b. Pairing in *P. Maudiae* is in 17 bivalents. Some disorders are visible at anaphase I.
 - c. Only 10.8 per cent of the *Maudiae* pollen grains are visibly non-viable. This does not give a true picture of the sterility of the plant.
6. Some conclusions are offered as to the several causes of sterility of the hybrid:
 - a. Inversions that give rise to anaphase I disorders.
 - b. An inversion, visibly terminal upon microscopic examination, which does not give rise to visible anaphase I disorders because it includes the centromere.
 - c. As a result of polyploidy in the genus some of the *callosum* chromosomes pair with themselves as do some of the *Lawrenceanum* chromosomes in meiosis of hybrid pollen mother cells. Some of the gametes are therefore deprived of necessary chromatin material.

LITERATURE CITED

Anon. (1912). *Cypripedium callosum* Sanderae. *Jour. Hort.* 65:565.
Black, J. M. (1933). Albinism in Cypripediums. *Orchid Rev.* 41:69-72.
Buser, R. (1894). *Cypripedium* ou *Cypripedium?* *Bull. Herb. Boiss.* 2:642-644.
Carson, H. L. (1944). An analysis of natural chromosome variability in *Sciara impatiens* Johannsen. *Jour. Morph.* 75:11-59.
_____, and Stalker, H. D. (1947). Gene arrangements in natural populations of *Drosophila robusta* Sturtevant. *Evolution* 1:113-133.
Cooper, E. (1946). White Cypripediums. *Orchid Rev.* 54:106-107.
Darlington, C. D. (1937). *Recent Advances in Cytology*, 2nd ed. Philadelphia.
Duncan, R. E. (1945). Production of variable aneuploid numbers of chromosomes within the root tips of *Paphiopedilum Wardii*. *Am. Jour. Bot.* 32:506-509.
_____, (1947). The hybrid Lady Slipper. *Orchid Dig.* 11:199-207.
_____, and MacLeod, R. A. (1948a). Chromosomes of the Brachypetalums. *Am. Orchid Soc. Bull.* 17:170-174.

_____, ____, (1948b). Chromosomes of the *insigne* complex of ladyslippers. *Ibid.* 424-429.

_____, ____, (1949a). The chromosomes of the continental species of *Paphiopedilum* with solid green leaves. *Ibid.* 18:84-89.

_____, ____, (1949b). The chromosomes of some of the Polyantha. *Ibid.* 159-163.

Francini, E. (1931). Ricerche embriologiche e cariologiche sul genere "Cypripedium". *Nuovo Giorn. Bot. Ital. N. S.* 38:154-212.

_____, (1932). Un reperto cariologico nella F₂ di "× *Paphiopedilum Lceanum*". *Ibid.* 39:251-253.

_____, (1934). Ibridazione interspecifica nel genere "Paphiopedilum." *Ibid.* 41:189-237.

Hooker, J. D. (1879). *Cypripedium Laurenceanum*. *Curtis's Bot. Mag. tab.* 632.

Kauffmann, B. P. (1936). A terminal inversion in *Drosophila ananassae*. *Proc. Nat. Acad. Sci.* 22:591-594.

Kossikov, R. V., and Muller, H. J. (1933). Invalidation of the genetic evidence for branched chromonemas. *Jour. Hered.* 26:305-317.

Mehlquist, G. A. L. (1947a). Polyploidy in the genus *Paphiopedilum* Pfitz. (*Cypripedium* Hort.), and its practical implications. *Mo. Bot. Gard. Bull.* 35:211-225.

_____, (1947b). Some smear techniques for counting chromosomes in orchids. *Ibid.* 229-233.

Meyer, J. R. (1943). Colchicine-Feulgen leaf smears. *Stain Technol.* 18:53-56.

Muller, H. J. (1938). The remaking of chromosomes. *Collecting Net* 13, No. 8.

Pfitzner, E. (1903). Orchidaceae-Pleonandreae. *Engler's Das Pflanzenreich*, IV, Fam. 50 (Heft 12).

Reichenbach, H. G. (1854). *Xenia Orchidacearum* 3.

_____, (1878). *Cypripedium Laurenceanum*. *Gard. Chron. II*, 18:748.

_____, (1885). *Lindenia* 1:89, pl. 42.

_____, (1886). *Cypripedium callosum*, n. sp. *Gard. Chron. II*, 26:326.

Rolfe, R. A. (1896). The Cypripedium group. *Orchid Rev.* 4:327-334; 363-367.

[_____,] (1900). *Cypripedium* × *Maudiae*. *Ibid.* 8:308.

Sander, C. F., F. K., and L. L. (1927). *Sander's Orchid Guide*. Rev. ed. Antwerp.

Sander, F. K. (1946). *Sander's Complete List of Orchid Hybrids*. St. Albans.

Stockwell, P. A. (1934). A stain for difficult plant material. *Science N. S.* 80:121-122.

Sturtevant, A. H., and Beadle, G. W. (1939). *An Introduction to Genetics*. Philadelphia and London.

Sutton, E. (1940). Terminal deficiencies in the X chromosome of *Drosophila Melanogaster*. *Genetics* 25:534-540.

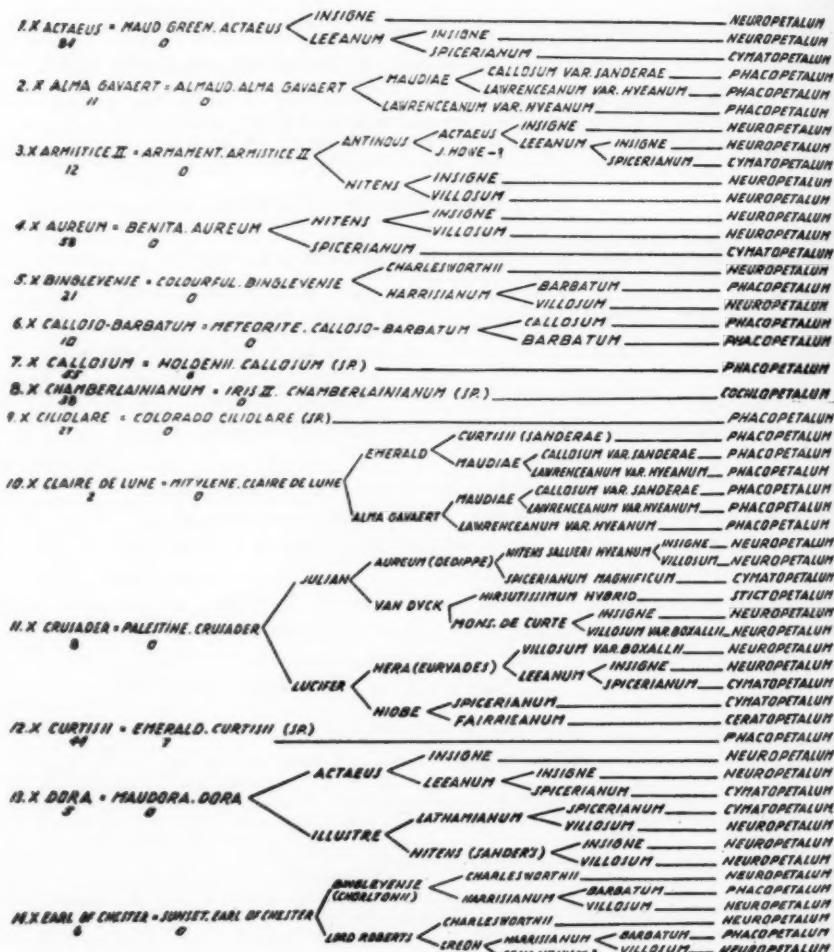
[Wilson, Gurney], (1933). *Cypripedium Maudiae*. *Orchid Rev.* 31:299-300.

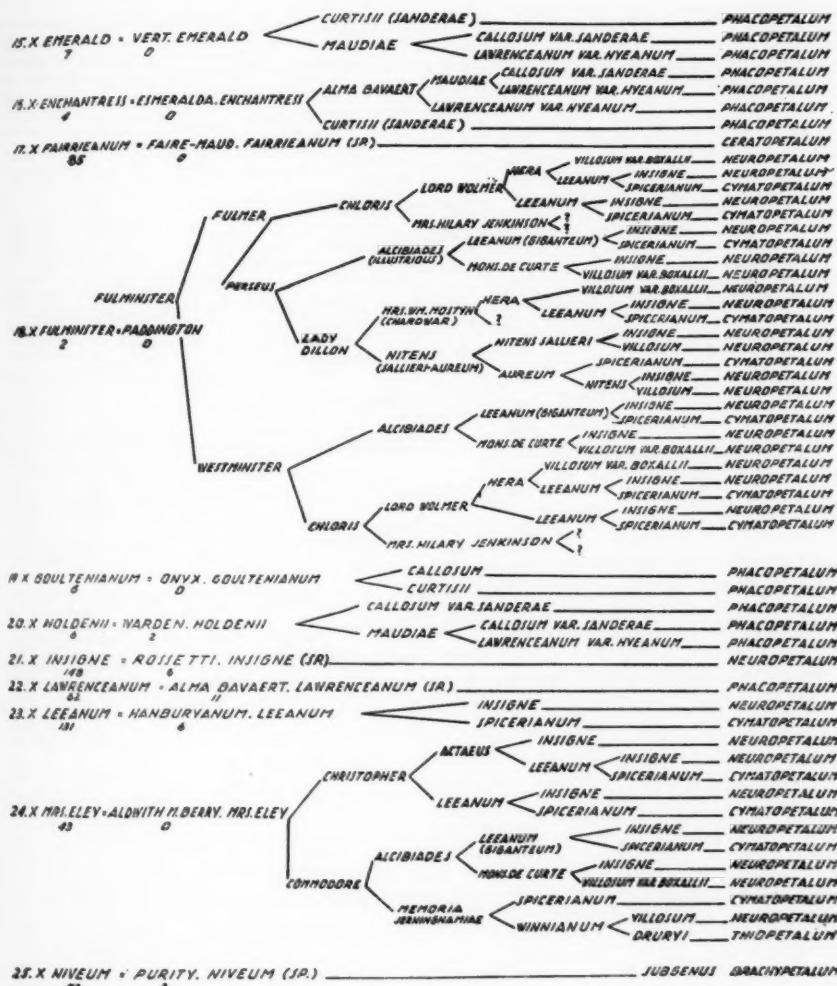
CHART I

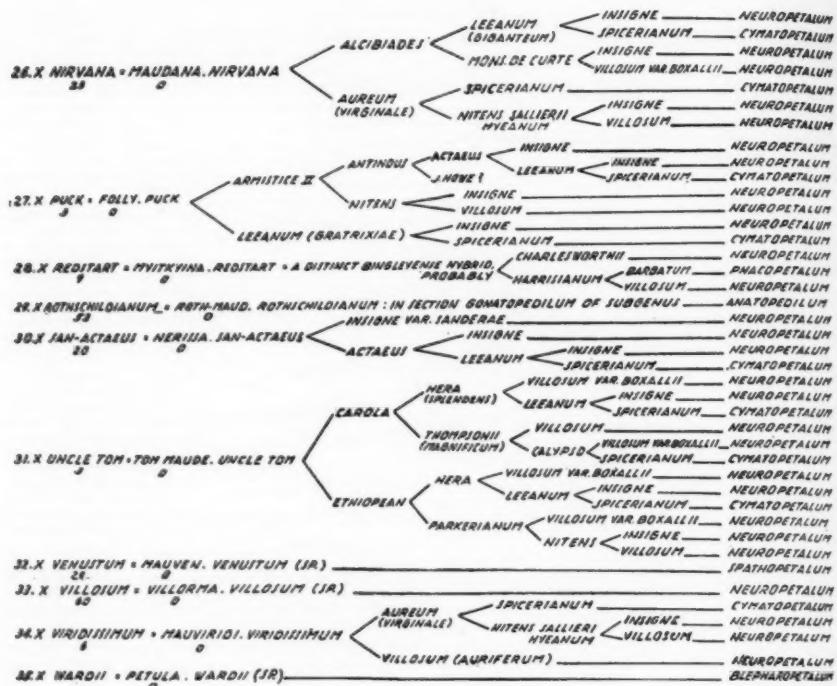
A LIST OF THE CROSSES IN WHICH *P. MAUDiae* HAS BEEN USED AS A PARENT.
THE NUMBERS BELOW EACH VARIETAL NAME INDICATE HOW MANY TIMES THE VARIETY HAS BEEN USED AS A PARENT.
TO THE RIGHT OF THE ANTECEDENT SPECIES ARE THE SECTION OF *OTOPEDILUM* OR THE SUBGENERA TO WHICH THEY BELONG.

MAUDIAE (SECTION PHACOPETALUM OF SUBGENUS OTOPEDILUM)
35

11







1949]

CHART II

LIST OF CROSSES IN WHICH *P. CALLOSUM* HAS BEEN USED AS A PARENT

Section of OTOPEDILUM (or other subgenera) used in cross	Species or hybrid used as parent*		Resulting progeny
1. PHACOPETALUM	× <i>ALMA GAVAERT</i> (Chart I #2)†	11‡	NEREID 0‡
2. PHACOPETALUM NEUROPETALUM	× <i>APPLETONIANUM</i> (App. Chart. II #1)	4	SIAMENSE 1
3. PHACOPETALUM	× <i>Argus</i>	40	CALLOSO-ARGUS 0
4. PHACOPETALUM NEUROPETALUM	× <i>ASHBURTONIAE</i> (App. Chart II #2)	12	ZENOBIA 1
5. NEUROPETALUM CYMATOPETALUM	× <i>AUREUM</i> (Chart I #11)	58	ALTRICHAMENSE 0
6. PHACOPETALUM	× <i>barbatum</i>	49	CALLOSO-BARBATUM 10
7. Subg. BRACHYPETALUM	× <i>bellatulum</i>	57	WOTTONII 1
8. NEUROPETALUM	× <i>Boxallii</i> (var. of sp. <i>villosum</i>)§	42	J. BARTELS 0
9. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	× <i>CALLO-ROTHSCHILDIANUM</i> (App. Chart II #3)	1	FRANCONIA 0
10. PHACOPETALUM SPATHOPETALUM	× <i>CALOPHYLLUM</i> (App. Chart II, #4)	13	PALLAS 2
11. COCHIOPETALUM	× <i>Chamberlainianum</i>	38	ALCIPPE 0
12. NEUROPETALUM	× <i>Charlesworthii</i>	66	ROSITA 0
13. PHACOPETALUM	× <i>ciliolare</i>	27	ZEUS 0
14. Subg. BRACHYPETALUM	× <i>concolor</i>	27	CONCO-CALLOSUS 0
15. PHACOPETALUM	× <i>Curtisia</i>	44	GOULTENIANUM 6
16. Subg. BRACHYPETALUM	× <i>Delenatii</i>	14	MME. MARTINET 1
17. THIOPETALUM	× <i>Druryi</i>	33	A. R. SMITH 0
18. NEUROPETALUM	× <i>exul</i>	20	DR. CONWAY 0
19. CERATOPETALUM	× <i>Fairrieanum</i>	85	JUNO 1
20. PHACOPETALUM NEUROPETALUM	× <i>gigas</i> (App. Chart II, #5)	8	E. J. SEYMOUR 0
21. Subg. BRACHYPETALUM	× <i>Godefroyae</i>	31	FELIX FAURE 0
22. PHACOPETALUM	× <i>GOULTENIANUM</i> (Chart II, #15)	6	MALHERBE 0
23. PHACOPETALUM	× <i>GOWERIANUM</i> (App. to Chart II, #6)	19	HORTENSE 0
24. PHACOPETALUM NEUROPETALUM	× <i>HARRISIANUM</i> (App. to Chart II, #1)	72	LEDOUXIAE 1
25. STICTOPETALUM	× <i>birdsutissimum</i>	33	DONCASTERIANUM 0
26. NEUROPETALUM	× <i>HITCHINSIAE</i> (App. to Chart II, #7)	17	SONIA 0
27. PHACOPETALUM	× <i>HOLDENII</i> (Chart II, #37)	6	GLORIOSUM 0
28. SPATHOPETALUM	× <i>Hookerae</i>	26	FORTUNA 0
29. NEUROPETALUM	× <i>insigne</i>	148	LEONIAE 2
30. BLEPHAROPETALUM	× <i>javanicum</i>	7	JAVA 0

*Species names are indicated in italics; hybrids, subgenera, and sections in caps.

†Key to explanations of varietal backgrounds are given in parentheses.

‡The figures following the names indicate the number of times the plant has been used in crosses.

§Treated as *P. villosum* var. *Boxallii* in Sander's 'Complete List of Orchid Hybrids'; treated as species *P. Boxallii* by G. A. L. Mehlquist (1947) and R. E. Duncan (1947).

Section of <i>OTOPEDILUM</i> (or other subgenera) used in cross	Species or hybrid used as parent*		Resulting progeny
31. <i>NEUROPETALUM</i> <i>CYMATOPETALUM</i> Subg. <i>BRACHYPETALUM</i>	× <i>J. M. BLACK</i> (App. Chart II, #8)	46	JAMES 0
32. <i>CYMATOPETALUM</i> <i>NEUROPETALUM</i>	× <i>LATHAMIANUM</i> (App. Chart II, #9)	39	CALLIOPE 0
33. <i>PHACOPETALUM</i>	× <i>Lawrenceanum</i>	62	MAUDIAE 35
34. <i>NEUROPETALUM</i> <i>CYMATOPETALUM</i>	× <i>LEEEANUM</i> (Chart I, #1)	132	ANGELIAE 0
35. ?	× <i>MADAME COFFINET</i>	2	MADAM MAXINE <i>OPOIX</i> 0
36. <i>BLEPHAROPETALUM</i>	× <i>Mastersianum</i>	24	PYTHO 0
37. <i>PHACOPETALUM</i>	× <i>MAUDIAE</i> (Chart I, #2)	35	HOLDENII 6
38. <i>NEUROPETALUM</i>	× <i>NITENS</i> (Chart I, #3)	66	WENDIGO 0
39. Subg. <i>BRACHYPETALUM</i>	× <i>niveum</i>	48	WINIFRED <i>HOLLINGTON</i> 1
40. <i>PHACOPETALUM</i> <i>NEUROPETALUM</i>	× <i>OENANTHUM</i> (App. Chart III, #2)	28	OLGA BOGSHAWE 0
41. Subg. <i>ANATOPEDILUM</i> Sect. <i>CORYOPEDILUM</i>	× <i>phillippinense</i>	22	MILLMANII 0
42. Subg. <i>ANATOPEDILUM</i> Sect. <i>CORYOPEDILUM</i>	× <i>Rothschildianum</i>	53	CALLO-ROTHS- <i>CHILDIANUM</i> 1
43. Subg. <i>ANATOPEDILUM</i> Sect. <i>CORYOPEDILUM</i>	× <i>Sanderianum</i>	13	PRINCESS MAY 0
44. <i>BLEPHAROPETALUM</i>	× <i>SEMENTA</i> (App. Chart II, #10)	8	AURELIANENSE 0
45. <i>CYMATOPETALUM</i>	× <i>Spicerianum</i>	62	MLE. GABRIELLE <i>MOENS</i> 0
46. Subg. <i>ANATOPEDILUM</i> Sect. <i>PRENIPEDILUM</i>	× <i>Stonei</i>	27	FORDIANUM 0
47. <i>PHACOPETALUM</i>	× <i>superbiens</i>	39	MOUSSETIANUM 0
48. <i>PHACOPETALUM</i>	× <i>SUPERCILIARE</i> (App. Chart II, #11)	18	MOREAUANUM 0
49. <i>PHACOPETALUM</i> Subg. <i>BRACHYPETALUM</i>	× <i>TAUTZIANUM</i> (App. Chart II, #12)	2	NANDII 0
50. <i>BLEPHAROPETALUM</i>	× <i>tonsum</i>	33	FELICITY 0
51. <i>PHACOPETALUM</i> <i>NEUROPETALUM</i>	× <i>TRIUMPHANS</i> (App. Chart II, #13)	1	RAJAH 0
52. <i>SPATHOPETALUM</i>	× <i>venustum</i>	29	ORPHEUS 3
53. <i>NEUROPETALUM</i>	× <i>villosum</i>	60	INDRA 0
54. <i>PHACOPETALUM</i> <i>BLEPHAROPETALUM</i>	× <i>WILLIAM MATTHEWS</i> (App. Chart II, #14)	1	ERNEST READ 2
55. <i>PHACOPETALUM</i> Subg. <i>BRACHYPETALUM</i>	× <i>WINIFRED HOLLINGTON</i> (App. Chart II, #15)	1	WINSUM 0

APPENDIX TO CHART II

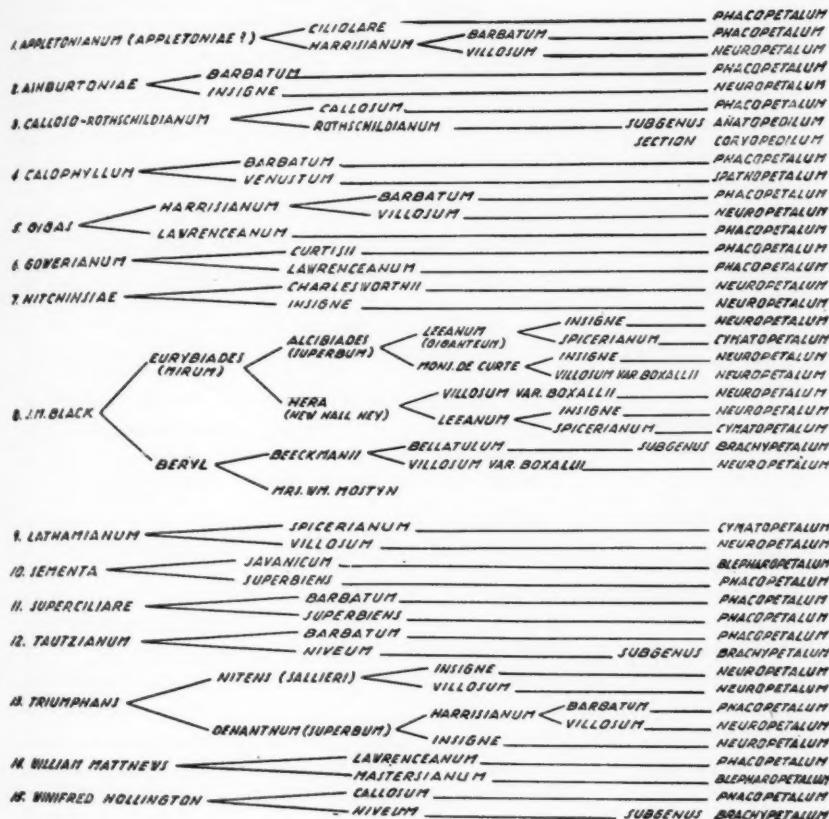


CHART III

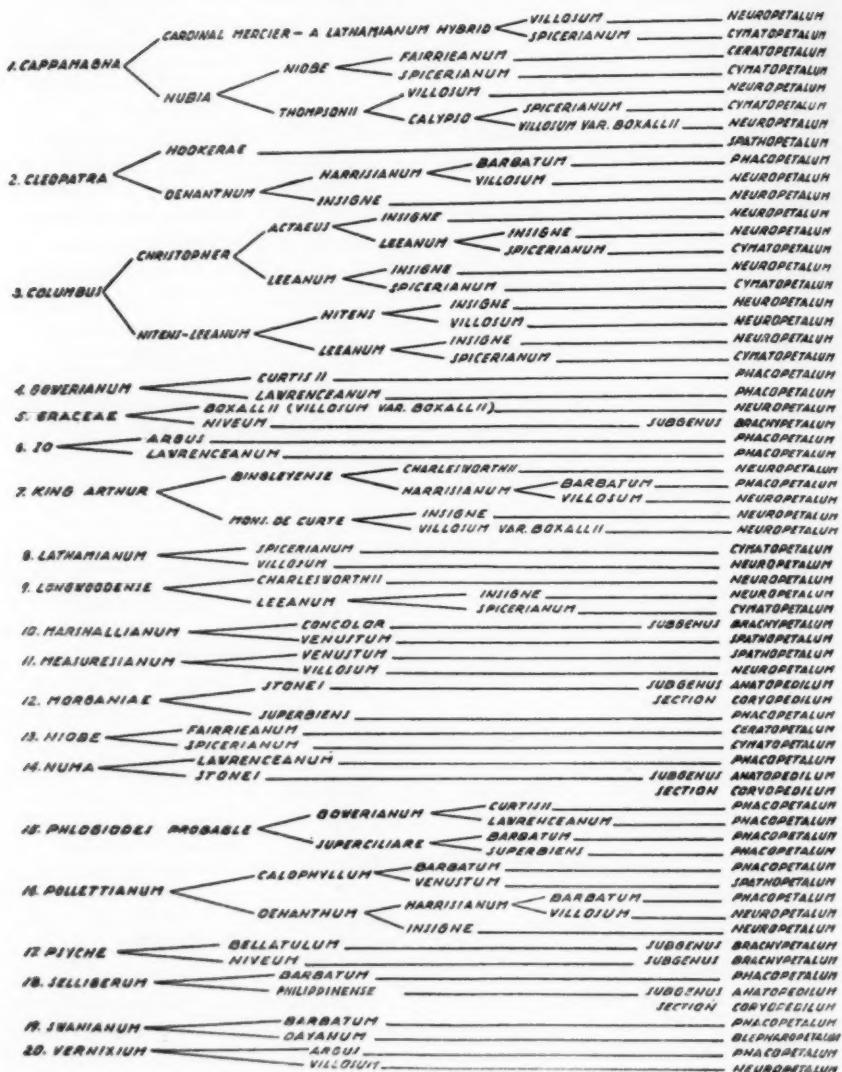
LIST OF CROSSES IN WHICH *P. LAWRENCEANUM* HAS BEEN USED AS A PARENT*

Section of OTOPEDIUM (or other subgenera) used in cross	Species or hybrid used as parent		Resulting progeny
1. PHACOPETALUM	× <i>ALMA GAVAERT</i> (Chart I, #2)	11	ELEANOR ROZILLA 0
2. PHACOPETALUM	× <i>Argus</i>	40	Io 15
3. PHACOPETALUM	× <i>barbatum</i>	49	ALMUM 3
4. Subg. BRACHYPETALUM	× <i>bellatulum</i>	57	LAURE-BEL 2
5. NEUROPETALUM	× <i>villosum</i> var. <i>Boxallii</i>	42	THAYERIANUM 0
6. PHACOPETALUM	× <i>CALLOSO-BARBATUM</i> (Chart I, #6)	10	MYTH 0
7. PHACOPETALUM	× <i>callosum</i>	55	MAUDIAE 35
8. NEUROPETALUM CYMATOPETALUM CERATOPETALUM	× <i>CAPPAMAGNA</i> (App. to Chart III, #1)	46	MONTROSE 0
9. COCHLOPETALUM	× <i>Chamberlainianum</i>	38	HIERO 0
10. NEUROPETALUM	× <i>Charlesworthii</i>	66	DECIPiens 0
11. PHACOPETALUM	× <i>ciliolare</i>	27	SMITHII 4
12. SPATHOPETALUM PHACOPETALUM NEUROPETALUM	× <i>CLEOPATRA</i> (App. to Chart III, #2)	1	RESPLENDENS 0
13. NEUROPETALUM CYMATOPETALUM	× <i>COLUMBUS</i> (App. to Chart II, #3)	11	SARDOW 0
14. Subg. BRACHYPETALUM	× <i>concolor</i>	27	CONCO-LAURE 0
15. PHACOPETALUM	× <i>Curtisii</i>	44	GOWERIANUM 19
16. BLEPHAROPETALUM	× <i>Dayanum</i>	26	LITTLEANUM 0
17. THIOPETALUM	× <i>Duryi</i>	33	CYBELE 0
18. NEUROPETALUM	× <i>exul</i>	20	JULIA 0
19. CERATOPETALUM	× <i>Fairriganum</i>	85	STREATHAMENSE 0
20. Subg. BRACHYPETALUM	× <i>Godefroyae</i>	31	DON CARLOS 0
21. PHACOPETALUM	× <i>GOWERIANUM</i> (App. Chart II, #6)	19	LAURE-GOWER 0
22. NEUROPETALUM Subg. BRACHYPETALUM	× <i>GRACEAE</i> (App. Chart III, #5)	2	GRIGNA 0
23. PHACOPETALUM NEUROPETALUM	× <i>HARRISIANUM</i> (App. to Chart III, #2)	72	GIGAS 8
24. STICTOPETALUM	× <i>birsutissimum</i>	33	MULAS 0
25. PHACOPETALUM	× <i>HOLDENII</i> (Chart I, #20)	6	PAULIAE 0
26. SPATHOPETALUM	× <i>Hookerae</i>	26	ENFIELDENSE 2
27. NEUROPETALUM	× <i>insigne</i>	148	UMLAUFIANUM 0
28. PHACOPETALUM	× <i>Io</i> (App. to Chart III, #6)	15	VANNINII 0
29. NEUROPETALUM PHACOPETALUM	× <i>KING ARTHUR</i> (App. Chart III, #7)	9	ERL KING 0
30. CYMATOPETALUM NEUROPETALUM	× <i>LATHAMIANUM</i> (App. Chart II, #9)	39	PYNAERTII 0
31. NEUROPETALUM CYMATOPETALUM	× <i>LEEEANUM</i> (App. Chart III, #3)	132	MAGNEI 0
32. NEUROPETALUM CYMATOPETALUM	× <i>LONGWOODENSE</i> (App. Chart III, #9)	18	VENIZELOS 0

*See footnotes Chart II for explanation.

Section of OTOPEDILUM (or other subgenera) used in cross	Species or hybrid used as parent		Resulting progeny
33. PARDALOPETALUM	× <i>Lowii</i>	20	MacFARLANIANUM 0 (If Macfarlanei = 1)
34. ?	× <i>L'YSER</i>	6	ALAIN GERBAULT 6
35. BLEPHAROPETALUM	× <i>Mastersianum</i>	24	WILLIAM MATTHEWS 1
36. Subg. BRACHYPETALUM SPATHOPETALUM	× MARSHALLIANUM (App. Chart III, #10)	1	HENRY GRAVES 0
37. PHACOPETALUM	× <i>MAUDiae</i> (Chart I, #2)	35	ALMA GAVAERT 11
38. SPATHOPETALUM NEUROPOETALUM	× <i>MEASURESIANUM</i> (App. Chart III, #11)	4	HEBE 0
39. Subg. ANATOPEDILUM Sect. CORYOPEDILUM PHACOPETALUM	× <i>MORGANIAE</i> (App. Chart III, #12)	11	VENETIA 0
40. CERATOPETALUM CYMATOPETALUM	× <i>NIOBE</i> (App. Chart III, #13)	28	WELLESLEYI 2
41. NEUROPOETALUM	× <i>NITENS</i> (Chart I, #3)	66	JOHNSONIANUM 0
42. Subg. BRACHYPETALUM	× <i>niveum</i>	48	ANTIGONE 2
43. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	× <i>NUMA</i> (App. Chart III, #14)	2	STANDENSE 0
44. PHACOPETALUM NEUROPOETALUM	× <i>OENANTHUM</i> (App. Chart III, #2)	28	BIJOU 0
45. MYSTROPOETALUM	× <i>Parisii</i>	5	ELIZABETHAE 0
46. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	× <i>pphilippinense</i>	22	CHARLES STEINMETZ 0
47. PHACOPETALUM	× <i>PHLOGIODES</i> (App. Chart III, #15)	1	NIGRUM 0
48. PHACOPETALUM SPATHOPETALUM NEUROPOETALUM	× <i>POLLETTIANUM</i> (App. Chart III, #16)	7	FABIA 0
49. Subg. BRACHYPETALUM	× <i>PSYCHE</i> (App. Chart III, #17)	15	CONOPUS 0
50. Subg. ANATOPEDILUM Sect. GONATOPEDILUM	× <i>Rothschildianum</i>	53	WIERTZIANUM 0
51. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	× <i>Sanderianum</i>	13	ULTOR 0
52. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	× <i>SELLIGERUM</i> (App. Chart III, #18)	21	LADY LLANGATTOCK 0
53. BLEPHAROPETALUM PHACOPETALUM	× <i>SEMENTA</i> (App. Chart II, #10)	8	CRASSIFOLIUM 0
54. CYMATOPETALUM	× <i>Spicerianum</i>	62	RADIOSUM 2
55. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	× <i>Stonei</i>	27	NUMA 2
56. PHACOPETALUM	× <i>superbiens</i>	39	EURYALE 5
57. PHACOPETALUM	× <i>SUPERCILIARE</i> (App. Chart III, #15)	18	AUGUSTUM 2
58. PHACOPETALUM BLEPHAROPETALUM	× <i>SWANIANUM</i> (App. Chart III, #19)	13	ROGERSII 0
59. BLEPHAROPETALUM	× <i>tonsum</i>	33	MADAM BARBEY 0
60. SPATHOPETALUM	× <i>venustum</i>	29	AUROREUM 2
61. PHACOPETALUM NEUROPOETALUM	× <i>VERNIXIUM</i> (App. Chart III, #20)	5	JULIEN COFFIGNIEZ 0
62. NEUROPOETALUM	× <i>villosum</i>	60	LURIDUM 0

APPENDIX TO CHART III



EXPLANATION OF PLATE

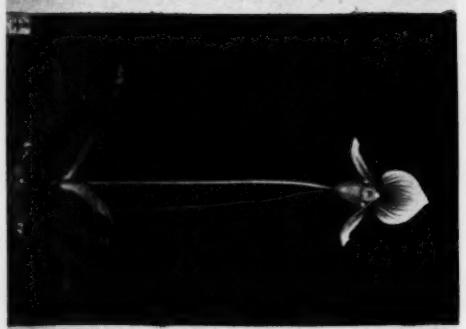
PLATE 31

Flowers about $\frac{1}{2}$; habits about $\frac{1}{4}$.

Figs. 1 and 2. *Paphiopedilum callosum*.

Figs. 3 and 4. *Paphiopedilum Maudiae* var. *magnificum*.

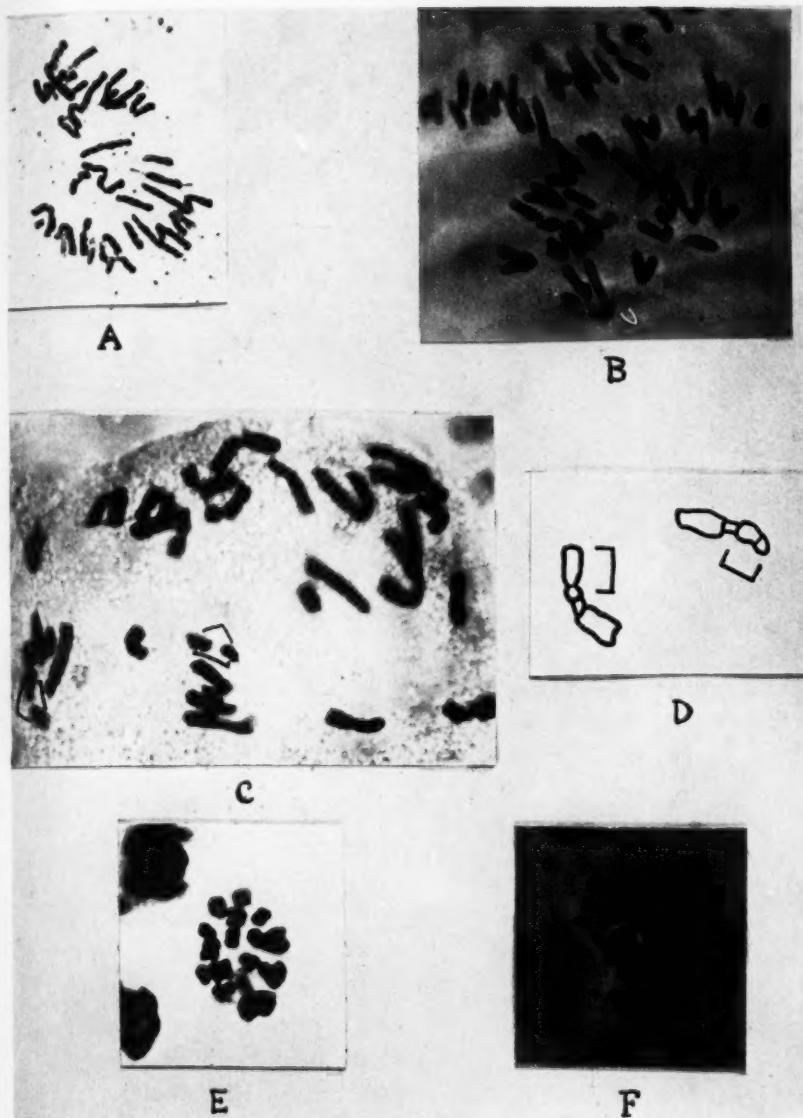
Figs. 5 and 6. *Paphiopedilum Lawrenceanum*.



EXPLANATION OF PLATE

PLATE 32

- A. Anaphase in root-tip of *Paphiopedilum callosum*, $\times 1350$. Aceto-lacmoid.
- B. Anaphase in root-tip of *P. Lawrenceanum*, $\times 1350$. Feulgen.
- C. Metaphase of root-tip of *P. Maudiae*, $\times 1350$. Feulgen. The two homologues showing the inversion are marked.
- D. Camera-lucida drawing of the chromosome pair showing an apparently terminal inversion. These chromosomes are of intermediate length and have a prominent secondary constriction. The centromere is subterminal in one and median in the other (centromere marked with a line). Magnification \times about 1800.
- E. *P. callosum*. Metaphase I, 16 bivalents, $\times 1350$. Crystal violet and safranin.
- F. *P. Lawrenceanum*. Metaphase II, 18 chromosomes, $\times 1350$. Crystal violet and safranin.

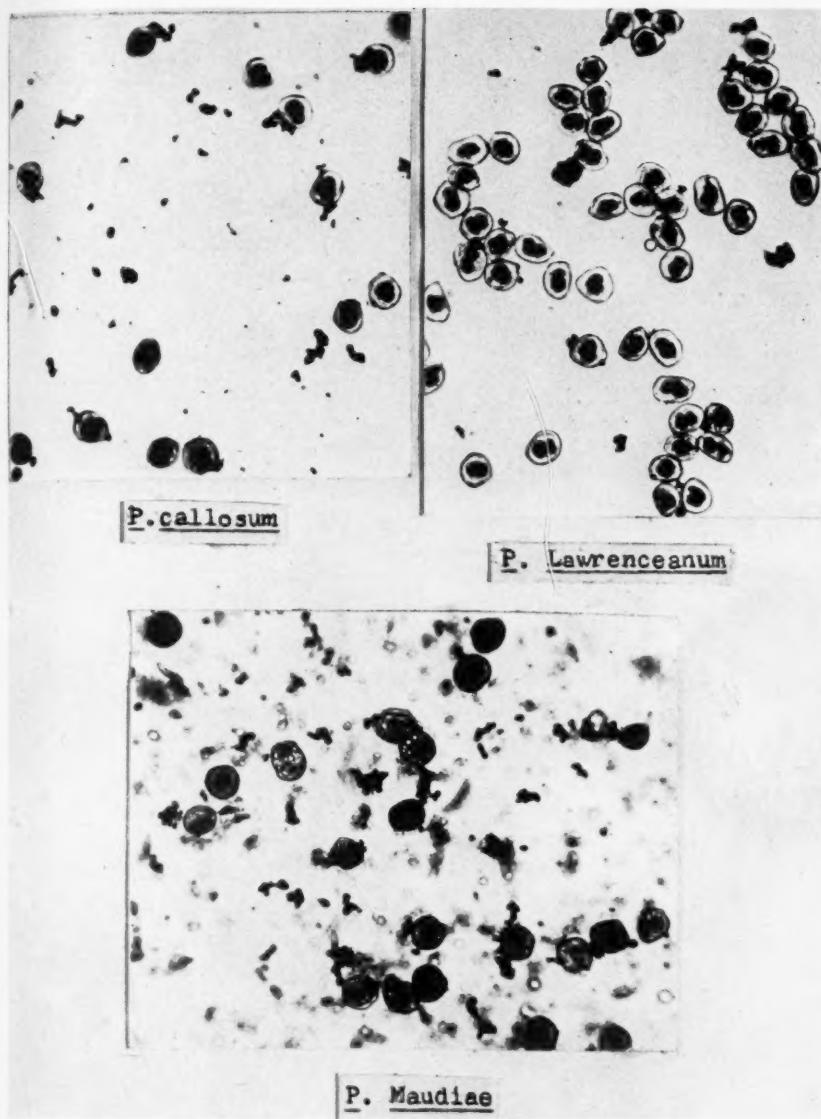


McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.

EXPLANATION OF PLATE

PLATE 33

Pollen of *Paphiopedilum callosum*, of *P. Lawrenceanum*, and of *P. Maudiae*, \times about 250.



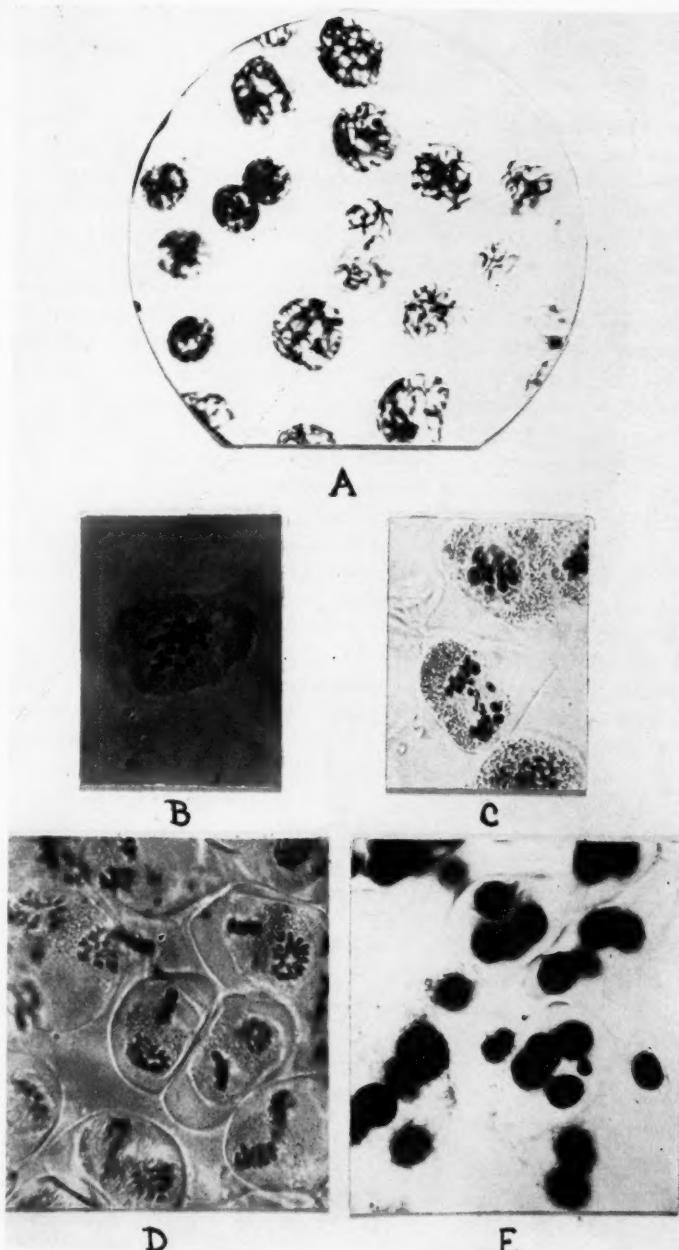
McQUADE—PAPHIOPEDILUM MAUDIAE HORT.

EXPLANATION OF PLATE

PLATE 34

Paphiopedilum Maudiae Hort.

- A. Pachytene-early diplotene, \times about 1350.
- B. Metaphase I, 17 bivalents, \times about 650.
- C. Anaphase I, bridge and fragment, \times about 650.
- D. Metaphase II, \times about 750.
- E. Tetrads (note micro-grain), \times about 700.

McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.



STEGNOSPERMA: A NEW SPECIES AND A GENERIC COMMENTARY

DAVID J. ROGERS

The genus *Stegnosperma* (Phytolaccaceae) has been considered monotypic since Walter's treatment for Engler's 'Pflanzenreich'¹. However, an examination of specimens in the major North American herbaria shows the inclusive species *S. balimifolium* Benth. of Walter to be rather heterogeneous. Actually, three species exist, two of which have been described and published, the third noted by S. Watson on an herbarium label but never published. A description of the third species is provided here and is named for Dr. Watson.

STEGNOSPERMA Watsonii D. J. Rogers, n. sp. *Frutices aut scandentes aut crassi patulique 1-5 m. alti, 1-5 m. diam., cortice griseo vel rufo-brunneo. Folia anguste spatulata vel elliptica emarginata vel rotunda vel acuta 1.0-3.5 cm. longa 0.5-2.5 cm. lata, petiolo 0.1-0.3 cm. longo. Inflorescentia cymulis axillaribus aut terminalibus 1-8-floris; calyx lobis ellipticis vel ovatis 0.3-0.7 cm. longis 0.2-0.4 cm. latis; petalis ovatis rotundatis basi abrupte constrictis; fructu capsula 5-loculata plerumque in 5 valvis dehiscente; seminibus plerumque 5 aliquando 4 ovoideis vel ellipsoideis circa 0.3 cm. longis 0.2-0.3 cm. latis, cicatrice funiculari laterali, raphe in jugum dorsalem, testa levi fulgenti rufo-brunneo.*

Sprawling vine or coarse spreading shrub, 1-5 m. tall, 1-5 m. diameter spread; bark gray to reddish brown. Leaves narrowly spatulate to elliptic, emarginate to rounded to acute, 1.0-3.5 cm. long, 0.5-2.5 cm. wide, petiole 0.1-0.3 cm. long. Inflorescence of axillary or terminal 1- to 8-flowered cymules; calyx lobes elliptic to ovate, 0.3-0.7 cm. long, 0.2-0.4 cm. wide; petals ovate, rounded, abruptly constricted at base; fruit a 5-celled capsule, usually dehiscing by 5 valves; seeds usually 5, occasionally 4, ovoid to ellipsoid, about 0.3 cm. long, 0.2-0.3 cm. wide, funicular scar lateral, raphe on a dorsal ridge, testa smooth, shiny, reddish brown.

MEXICO: BAJA CALIFORNIA: Wiggins 7681. SINALOA: Jones s. n. SONORA: Abrams 13343; Coville 1646; Dawson 1058; Dronet, Richards & Alvarado 3443; Ferris 8741; Gentry 2195, 2975; Goldman 399; Keck 4067; LeRoy s. n.; Lumboltz 9; McGee s. n.; William Palmer 1226 (HOLOTYPE in Herb. Missouri Botanical Garden, isotypes in Herb. N. Y. Bot. Gard. and U. S. Nat. Herb.); Pringle s. n.; Rose 1211, 1211a; Rose, Standley & Russell 12390, 12566, 13138, 13231, 15047; Shreve 5992; Wiggins 6247.

This species seems to be most closely related to *S. balimifolium* Benth., from which it may be distinguished by its scattered, few-flowered cymules, its ovate, abruptly constricted petals, and by its lateral funicular scar.

Stegnosperma Watsonii grows on hillsides along rivers, thickets in palm groves, thorny foothills, from sea level to 300 meters. It flowers from about the first of February through March, and fruits from the last of February through April.

That there are actually three species of *Stegnosperma* is most easily demonstrated by the following key:

¹Walter in Engl. Pflanzenr. IV, 83:124. 1909.

Issued November 30, 1949.

- A. Inflorescence a terminal, many-flowered racemiform thyrs; petals rather gradually narrowed to the base.
- B. Sepals linear to elliptic; petals linear to spatulate; capsule dehiscing by 3 to 4 or rarely 5 valves, usually with 1 to 3 seeds; seeds with a lateral to sub-basal funicular scar, the raphe on a flattened dorsal surface..... *S. cubense*
- BB. Sepals ovate; petals ovate to elliptic; capsule dehiscing by 5 valves, usually with 5 seeds; seeds with a basal funicular scar, the raphe on a dorsal ridge..... *S. halimifolium*
- AA. Inflorescence an axillary, 1- to 8-flowered cymule; petals abruptly constricted at the base *S. Watsonii*

STEGNOSPERMA CUBENSE A. Rich. in Sagra, Hist. Nat. Cuba 10:309; 12:tab. 44³. 1845.

[*Trichilia*] *scandens*, *foliis simplicibus*, *ovatis alternis*, etc. A. Robinson ex Lunan, Fl. Jam. 2:319. 1814.

Trichilia scandens Lunan ex B. D. Jackson, in Index Kewensis 2:1105. 1895. Based on the preceding.

Stegnosperma scandens (Lunan ex B. D. Jackson) Standley, in Field Mus. Publ. Bot. 23:6. 1943.

Stegnosperma halimifolium of authors, not Benth.

MEXICO: TRES MARIAS ISLANDS: Fisher s. n.; Howell 10409; Maltby 45; Mason 1702; Nelson 4185; Solis 4, 22, 45. REVILLA GIGEDOS ISLANDS: Mason 1846. SINALOA: T. S. Brandegee s. n.; Eyerdam & Beetle 8652; Lamb 465; Mexia 45, 152, 1095; Ortega 4480, 5150, 5649, 6453, 7232, 7488; E. Palmer 1503; Rose s. n., 1535; Rose, Standley & Russell 13721. NAYARIT: Ferris 5309; Nelson 4349. COLIMA: Goldsmith 99; Jones 13; E. Palmer 1280. MICHOACAN: Hinton 12627; Leavenworth & Hoogstraal 1394. MEXICO: Hinton 3764. GUERRERO: Hinton 5431, 5719, 5962. OAXACA: Matuda 0664; Nelson 2597; Orcutt 3307. CHIAPAS: Matuda 2808; Morley 710. VERA CRUZ: Purpus 8959, 10989, 13066.

GUATEMALA: ESCUINTLA: Salas 378. SAN JOSE: Worth, Morrison & Horton 8632. RETALHULEU: Standley 87707. SAN MARCOS: Steyermark 37762, 37773, 37881. SUCHITEPEQUEZ: Steyermark 47825. ZACAPA: Standley 74066; Steyermark 42084.

EL SALVADOR: LA LIBERTAD: Standley 23219.

NICARAGUA: CHINANDEGA: Baker 2065. MANAGUA: Chaves 262; Garnier 1071; Maxon, Harvey & Valentine 7215.

CUBA: HABANA: Ekman 13493. PINAR DEL RIO: Baker & Van Hermann 4247; Ekman 13039, 16733; Leon & Roca 7132, 8810; Shafer 11140, 11148; Wilson 11400, 11404. WITHOUT LOCALITY: Wright 2027.

JAMAICA: vicinity of Spanish Town, Britton 3062. Healthshire Hills, Harris & Britton 10522.

DOMINICAN REPUBLIC: Beata Island, Fairchild 2605, 2606, s. n.; Ostenfeld 319. Massif des Cahos, Ekman H9095. BARAHONA: Ekman H9061. SIERRA DE OCOA: Ekman H13360. WITHOUT LOCALITY: Bertero s. n.

PUERTO RICO: Asomante, Horne & Britton 9628.

This species, although placed in synonymy under *S. halimifolium* by Walter², is sufficiently distinct to be maintained. The description and plate provided by Richard demonstrate its characters accurately. Further characters which support my interpretation are found in the seed. These characters are used in the key.

An interesting nomenclatorial problem concerning this species arose when Standley³ made an apparently valid transfer of a "species" of *Trichilia* ascribed to Lunan by B. D. Jackson in 'Index Kewensis'⁴. Lunan's "publication" of A. Robin-

² Walter, loc. cit.

³ Standley, in Field Mus. Publ. Bot. 23:6. 1943.

⁴ B. D. Jackson in Index Kewensis 2:1105. 1895.

son's manuscript description of a new species of *Trichilia* was as a polynomial. Jackson's interpretation of the name as a binomial possibly could be explained by a method used in early printing in which the first word of a page was placed at the bottom of the preceding page on a line by itself. In this case, the first word to appear in the first sentence at the top of page 320, Lunan's Fl. Jam. Vol. 2, and accordingly at the bottom of the preceding page was "scandens." I do not think that Lunan intended a binomial since he did not mention "scandens" as a species in his Classical Index of this work although other properly published binomials are listed, nor did he use the same form in his discussion of the plant in question as he consistently used throughout the text for species designation.

STEGNOSPERMA HALIMIFOLIUM Benth. Bot. Voy. Sulph. 17: pl. 12. 1844 (as *balimifolia*).

MEXICO: BAJA CALIFORNIA: T. S. Brandegee s. n.; Carter 2725; Carter, Alexander & Kellogg 1980, 2115, 2497; Collins, Kearney & Kempton 186; Epling & Robison s. n.; Ferris 8617; Gentry 4032, 7603, 7864; Hammerly 102; Harvey 609; Johnston 3166, 3354, 3488, 3512, 3593, 3825; Jones 24481, 27465; Nelson & Goldman 7147, 7249, 7323, 7395, 7502; E. Palmer 31, 258, 400, 870; Purpus s. n., 5; Rose 16289, 16415, 16616, 16690; 16924; 16947; Shreve 6973; Wiggins 5415, 5651, 6070, 7793; Xantus 9b. SONORA: MacDougal & Shreve 40, 47; Pringle s. n.

The generic ending of Bentham's specific epithet has been altered to comply with the International Rules of Botanical Nomenclature, Section 14, Art. 72 (2).

As I have interpreted this species, it occupies a rather narrow range in Baja California and occasionally in the adjoining state of Sonora, Mexico.

I have been able to examine specimens from several of the major herbaria of the United States, but have not seen the type specimens nor any other material from Europe.

The herbaria where specimens have been obtained for study are as follows: Gray Herbarium of Harvard University, Chicago Natural History Museum, Missouri Botanical Garden, New York Botanical Garden, University of California at Berkeley, and the United States National Herbarium.

I wish to acknowledge my indebtedness to the curators of these institutions.

NUCELLANGIUM, A NEW GENUS OF FOSSIL SEEDS PREVIOUSLY
ASSIGNED TO LEPIDOCARPON

HENRY N. ANDREWS, JR.

Among the more abundant fossils found in the Iowa coal balls are the highly unique "seeds" which have been named *Lepidocarpon glabrum*. These were described by W. C. Darrah in 1941, and in a more recent publication (1949) the same author has continued the discussion with descriptions of included structures which are claimed to be gametophytes and embryos. It is the purpose of this paper to add somewhat to the information given in the published accounts, to point out what appear to the present writer as erroneous statements of fact, and to correct the corresponding conclusions. The fossil is not referable to any known genus, and a new generic name, *Nucellangium*, is proposed herewith for its reception.

Origin of the specimens.—

The specimens on which the present descriptions are based were collected by Mr. Frederick O. Thompson from the Urbandale coal mine located on the western outskirts of Des Moines, Iowa, the exact location having been given in the results of a previous study from this laboratory (Andrews and Kernen, 1946). It should be noted that these specimens and the ones described by Darrah come from the same locality, and through the cooperation of Dr. Elso Barghoorn I have also been able to study a series of similar preparations from the Botanical Museum of Harvard University. There is, therefore, no possibility of confusion in the identity of Darrah's specimens and the ones on which this account is based.

The material is from beds of Middle Pennsylvanian (Des Moines) age; unfortunately the precise stratigraphical equivalence of the Urbandale coal is not known but presumably the material is a little younger than floras known from Illinois No. 6 coal or from above the upper Freeport coal of Pennsylvania.

General introduction to the nature of the fossils.—

We are involved in this discussion with two sets of fossil plants, the first being ovoid bodies presenting certain anatomical characters which lend some justification to their being considered as seeds, and the second less regularly shaped bodies with highly distinctive convolutions extending into their interior which are alleged to represent gametophyte and sporeling.

Certain competent botanists who have examined the fossils in my collection have expressed doubt that the two phases or forms belong to the same species. Mr. Darrah has based his case on the supposition that they represent different growth stages of the same organ. I agree with him to that extent yet it must be remembered that it is not beyond the realm of possibility that we are wrong in this belief.

It seems most convenient to refer to these two forms as *proliferated* and *normal* depending on whether they do or do not contain the supposed sporelings. In view

of the incomplete nature of the previously published accounts it will be necessary to present rather detailed descriptions of the two phases.

I have little doubt that many morphologists will take issue with the usage of terms as they are applied to these fossils. It is becoming clear, however, in groups such as the psilophytes and early coenopterid ferns, that the fossils are not going to make a special effort to comply with our preconceived terminology. It is hoped that the following pages contain descriptions that may be readily comprehended, but I believe that these fossils present structures which do not correspond precisely with known morphological entities.

Insofar as the evidence allows it seems clear that the fossils are sporangia that may or may not have been integumented. It is not known how they were borne on the parent plant and Darrah's restoration of the "strobilus" (1949, fig. 39) is based, so far as I am able to judge, on the supposed general lycopod affinities of the fossil rather than on conclusive evidence. There is a trace of conservatism in the caption to that figure which reads, "Sporophylls not sufficiently known to warrant reconstruction." The fact is that nothing whatsoever is known of the supposed sporophylls.

The general organization of the fossil, with its vascularization and complicated wall structure, seems to allow a closer comparison with a cordaita seed than with a lycopod sporangium. We shall return to such speculations on a later page.

The fossil will be referred to in the following pages as a *sporangium*, as a *nucellus*, or as an (unintegumented) *seed*. The last term is used advisedly and as a matter of convenience, although it seems probable that at least the specimens containing a "seed megasporangium" did function as such. It seems most expedient to present first a detailed description of the "normal" fossils and then consider the morphology of the principal structures involved.

The "normal" seeds.—

These are very abundant in the Urbandale coal balls as well as in those from other localities which probably represent the same or a close horizon. In many of the coal-ball specimens examined a half dozen or more are exposed in a single saw cut and, due to the distinctive structure and preservation of the epidermal layer, they are often partially exposed on the broken surfaces of the petrifications. It is occasionally possible to isolate the seeds intact from the surrounding matrix. While the following description is supplemented by observations on dozens of specimens it is based primarily on a series of transverse sections prepared through a single specimen.

Although there is some variation in the size of the specimens it is not great. They are broadly ovate (figs. 1, 2), averaging 12 mm. long, and in the median region the large and small diameters are 9.5 by 6 mm. Many specimens, particularly the more poorly preserved ones, are crushed and distorted, yet there can be no doubt that the shape and dimensions as given here represent the life form of the seeds.

At one end of these slightly elongated structures, which we will refer to as the proximal end, there is a tiny circular "hilum" scar (fig. 5) representing the point of attachment. At the other end, which will be referred to as the distal end, the seed tapers to a blunt point. Fairly conspicuous ridges lead to this point from the median region of the seed, following the narrow lateral faces. The specimens shown in figs. 1 and 2 present the broad side of the seed and the ridges here form the outline of the photo of the upper half of the seed. The hilum scar may be seen at the proximal end in fig. 1 and the blunt point at the opposite extremity.

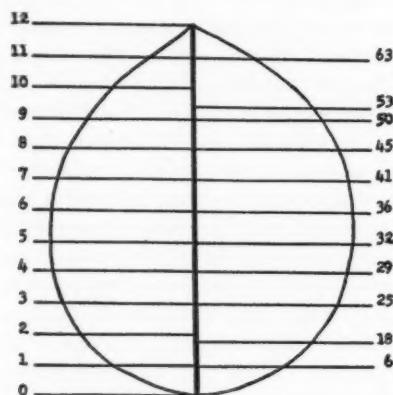
A series of peel preparations has been made by first carefully smoothing a flat surface at the hilum end. Seventy successive peels were then made to within less than a half mm. of the distal end. Particular care was taken to obtain a nearly perfect serial series at the hilum end in order to trace accurately whatever vascular system might be present. When it became evident after working through about one quarter of the length of the specimen that sudden changes in anatomy were no longer taking place the sections were taken further apart in the median region.

It is perhaps apparent that this is a case in which the peel technique is quite indispensable, for it would be only through the greatest good fortune and the use of numerous well-preserved specimens that somewhat comparable results could be obtained by reliance only on ground sections. It is probable that if the specimen had been properly imbedded even better preparations could have been made. However, they were generally removed with little difficulty by using a sharp razor under the low power of a dissecting microscope. Occasionally the epidermis was partially destroyed but since this remains constant in structure from one end to the other there was no loss. Text-fig. 1 indicates the approximate position from which the respective peels were taken.

To present an effective description of *Nucellangium* this series of preparations will be followed from proximal to distal end. It may be an aid in following the discussion to note at the outset that three characters set this fossil apart from previously described species of *Lepidocarpon*. These are: a well-developed vascular system with two strands running nearly the entire length of the seed; a thick complex wall including an inner sclerotic layer; and a mode of attachment unlike that of the radially elongated sporangia of other species of *Lepidocarpon*. This combination of characters, and particularly the vascular system, clearly prevents the inclusion of the fossil in that genus.

In the first peel prepared, which does not quite reach the inner limit of the epidermis, the central vascular strand may be distinguished. It is circular in transverse section and is composed of a considerable number of conducting elements (fig. 8). It is apparently purely tracheidal, no parenchyma cells having been observed. The conducting elements of this basal strand, as well as those of the lateral traces, are distinctive in that they are thin-walled, follow a slightly sinuous course, and the bands composing the secondary thickenings are fine and delicate, a condition, judging from the generally good preservation through the specimen, that is natural and not the result of decay. It is not possible to determine

whether the secondary thickenings were of a typical annular or scalariform nature; if the latter, it seems evident that the border of the thickenings was not strongly developed.



Text-fig. 1. Diagrammatic longitudinal view presented as an aid in following the description of the series of transverse peels described on the accompanying pages. Figures at left are millimeters; figures at right represent peel numbers.



Text-fig. 2. Diagrammatic median longitudinal section through the major axis of the seed showing the entrance of the vascular strand at the base and the course of the two branch traces through the length of the wall.

At peel No. 4 a disturbance of the thin-walled parenchyma surrounding the strand suggests a departing trace and when peel No. 6 is reached the tracheids of a branch trace may be observed, not actually leaving the strand but more than half way to the periphery of the seed. At first it was thought that the point of departure had been missed but in the next peel the trace was noted both departing (fig. 6) and in the outer region, as noted above. It is evident, as shown in fig. 10, as well as in text-fig. 2, that the trace dips down slightly after leaving the central strand to follow its course up through the seed. In peel No. 7 the departure of a second trace appears on the opposite side of the central strand.

No other branch traces were observed although a careful search was made, since in his original description Darrah (1941) notes, with reference to the vascular system: "At the proximal end of this seed-like sporangium there is a vascular trace which forks twice, but the four branches quickly exhaust themselves. The bifurcations are at right angles to each other, and by serial sections it has been observed that the two forkings take place one above the other." (p. 97).

The presence of these vascular strands, as I have described them, is of the greatest importance since they are typically absent from lycopod sporangia. It is understandable that they might be readily overlooked in longitudinal sections but

I cannot feel that there is adequate excuse for failing to observe them in the serial sections Darrah indicates were prepared (1941, p. 85).

The pair of traces continues to within less than one half mm. of the distal end of the seed and may be clearly observed in most of the peels throughout the length of the seed; and in the specimen described here there is no suggestion of a second pair of traces. A possible explanation of the *apparent* departure of such will be offered below.

It is clear from all of these transverse peels, with the exception of the basal two or three, that the seeds are bilaterally symmetrical in their anatomy as well as in their gross external form. Taking as an example a nearly median section (fig. 16) the ovate form of the fossil is evident and the two traces may be seen at either end of the great diameter, the traces in this peripheral region occupying a position in extensions of the inner sclerotic layer. Figure 7 shows the trace rather well at a point where it and the surrounding tissues are quite well preserved.

For the purpose of considering the extra-vascular structure of the seed a nearly median point will be taken where a typical sequence of the tissues is displayed. Selecting peel No. 34 (figs. 12, 16) the following may be clearly defined:

The thick-walled, palisade-like epidermis (fig. 9) forms the outer cell layer of the seed over its entire surface with the exception of the hilum scar at the base. These cells are arranged with their long axis approximately parallel to a radius of the seed. They are uniform in size and shape, being about 125μ long and, when observed in surface view, about 25μ in diameter. These cells also present an interesting preservation problem. They seem immune to the action of hydrochloric acid, unsuccessful attempts having been made to etch the outer face in order to obtain surface peels. Apparently they are little, if at all, mineralized. It is not surprising that with such an external tissue, so seemingly resistant to an infiltrating mineral solution, the more delicate internal tissues are poorly preserved in most specimens.

Within this epidermal layer is a broad zone of nearly isodiametric, rather thin-walled cells (the outer parenchyma, o. p. of figs. 12, 16). As may be noted in the photos this tissue comprises a major portion of the sporangium wall as a whole. There is a tendency for approximately the outer third of this tissue to have somewhat thicker cell walls than the inner region although there is no sharp distinction into two zones. It is highly significant to the discussion of the morphology of the seed to note that this is clearly *in continuous tissue connection with the conspicuous columnar epidermis*.

Forming a third layer is a very prominent, dark and semi-sclerotic tissue (inner sclerotic layer, i. s. of figs. 12, 16). The term "sclerotic" is perhaps misleading although the cells are somewhat thicker walled than those of the outer parenchyma.

It will be noted (fig. 12) that the cells of this tissue increase appreciably in diameter towards the inner periphery, and they are longitudinally elon-

gated, being at least twenty times as long as they are broad. Where the preservation is good, and nearly perfect longitudinal sections are obtained, the cell walls appear to be strongly pitted. The end walls are transverse or only slightly oblique. The pits (fig. 4) are generally more or less oval-shaped and apparently simple, but whether an actual membrane separated one cell from the next in life cannot be determined. The pitting in some cells is more complex and may even approach reticulate banding. In certain of the more proximal sections in the series of peels taken through the specimen some of the cells of this tissue resemble the tracheidal cells of the traces. It is my suggestion that Darrah may have mistaken these for the second pair of traces mentioned in his account.

The abundant pitting of these cells and their great length as compared with the other non-vascular tissues suggest that their primary function was the conduction of fluids. In studying the seed from base to apex the presence of this tissue is first noted at the level of peel No. 7. From this point to approximately peel No. 11 it develops in abundance in two separate groups, sheathing the departing traces. The two groups soon expand in two C-shaped masses until they unite as a continuous band at the level of peel No. 29. The radial width of this band thereafter gradually increases as is shown in text-fig. 3.

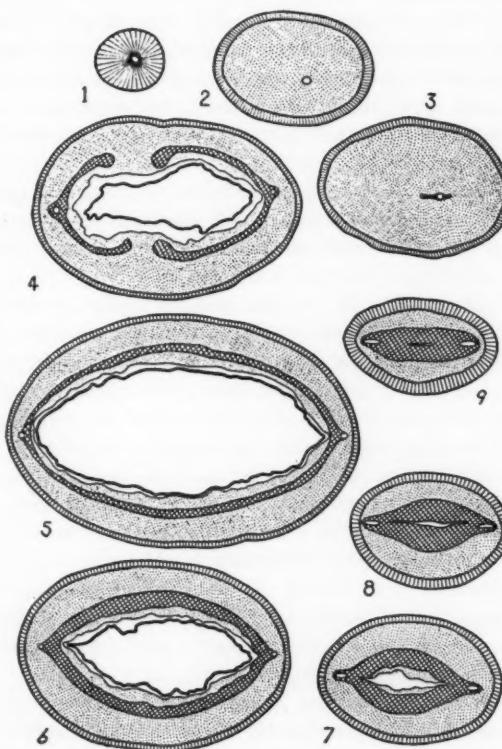
Within the sclerotic layer there is a fourth tissue consisting of very thin-walled cells which in most specimens has been lost through decay. In a few instances, however, it is possible to observe that this tissue did consist of rather thin-walled parenchymatous cells.

Within this fourth tissue layer it is possible, in most sections of the series, to follow a distinct, light yellow band around the periphery of the central cavity. The presence of this structure has been checked in numerous other specimens, and there seems to be no doubt that it is correctly identified as the megaspore membrane. Darrah has succeeded in isolating it very nicely by maceration, a fine illustration being given in his 1949 paper (fig. 11).

No tissue has been observed within this megaspore membrane. The shape of the internal cavity will, however, be described briefly. In following the series of transverse sections from proximal to distal end, at peel No. 10 a small cavity appeared in the position occupied in previous peels by the trace and its accompanying tissue. In peel No. 15 a similar cavity made its appearance on the opposite side and in peel No. 17 the two cavities merged. The fact that one cavity appeared before the other is due to a very slight obliquity in the internal structure of the seed, possibly a slight aberrancy of the particular specimen.

It thus appeared from a study of the serial sections that the internal cavity would be heart-shaped if viewed in median longitudinal section. It has been possible to confirm this supposition from such a nearly median section in the collections of the Harvard Botanical Museum. The basal portion of the specimen is

shown in figure 10. This is a trifle oblique to the median plane so that the actual entrance of the trace into the seed is not shown. The trace does appear, however, as a conspicuous mass of tracheids (fig. 10, t), flaring upwards and terminating the upper part of the cushion or "archesporial pad." A portion of one of the two traces is shown curving down and upward to the left in the outer parenchymatous tissue.



Text-fig. 3. A series of diagrams prepared from representative points in the series of transverse peels described on pages 480-484. 1, peel No. 1; 2, peel No. 3; 3, peel No. 8; 4, peel No. 20; 5, peel No. 38; 6, peel No. 53; 7, peel No. 64; 8, peel No. 66; 9, peel No. 69. Outer lined area, epidermis; stipple, outer parenchyma; cross-hatch, inner sclerotic tissue; inner stipple, inner parenchyma; heavy inner line, megasporangium. In 1 only the epidermis and central strand are shown; in 2 the epidermis, outer parenchyma, and central strand; in 3 the epidermis, outer parenchyma, central strand, and beginnings of the inner sclerotic tissue; 4-6 present the complete sequence of tissues with the traces shown at either end of the long transverse axis; 7 is taken above the distal limit of the megasporangium.

Before leaving this description of the normal seeds I feel compelled to add a comment on Mr. Darrah's recent paper in which he sums up the distinctive features of these fossils: "Thus far in the development of the sporangium there are no structures or tissues which are unusual. Externally, there is the sporangium wall of usual lepidodendrid construction innermost the megasporangium, which can be removed easily by maceration. The tissues between are sterile sporogenous tissues." (1949, p. 3). I do not understand the last sentence but to state that the sporangium wall with its thickness, its complex series of tissues, its vascularization, and its mode of attachment is "of usual lepidodendrid construction" certainly displays a taxonomic freedom that might allow the inclusion of anything within the genus *Lepidocarpon*. Darrah notes further that "My preference for broad rather than narrow interpretations of genera is well known." (p. 12). But surely somewhere there must be limitations.

I feel certain that there is nothing in the literature of lycopod sporangia, living or fossil, which presents a close comparison with this fossil. It is clearly far beyond the bounds of Scott's generic description for *Lepidocarpon* (Scott, 1901) and bears no resemblance to *L. lomaxi*, the type of the genus.

It is perhaps obvious that the principal problem that is involved in correctly interpreting the morphology of this fossil is whether we are dealing with a sporangium or whether it is a true seed. That is, whether the structure described above is a sporangium ("nucellus") enclosing a single fertile megasporangium, or whether it is an integument enclosing the remains of a nucellus and the megasporangium. I am of course following Darrah's interpretation in accepting the former choice. The reasons for this are as follows: There is no break in the continuity of the four tissues composing the wall of the fossil. They are all clearly in organic connection, there is no delimiting epidermal layer on the inside, and between this innermost parenchymatous layer and the megasporangium there is no structure that might be interpreted as the remnants of a nucellus. Furthermore, there is no evidence that a micropylar opening existed at the distal end of the fossil. The tissue appears to be continuous here, allowing access of microspores only by a dehiscence of the sporangium, presumably along the lateral ridges.

Although the outer epidermal layer is very resistant, the shape of the cells and their alignment are as closely comparable to the prismatic epidermis of many cryptogamic sporangia as they are to the epidermis of seed integuments. It has long been recognized that the nucellus, in fact, is a modified sporangium and an epidermal layer so strongly suggestive of its sporangial homology is not surprising in a form that, as far as we know, probably lacks integuments completely.

The "proliferated" seeds.—

Associated with the above-described normal seeds in the Iowa coal balls from the Urbandale mine are other fossils of an even more problematical nature. I believe that they present, as Darrah indicates, a different growth stage than that of the normal specimens. It is freely admitted by the present writer that he is certain of neither their natural affinities nor their morphology but evidence will be

offered to support the contention that the structures described as "gametophytes" and "sporelings" are morphologically one and the same and that they constitute proliferations of sporangial wall tissue.

In the Urbandale coal balls that have passed through my hands some two or three dozens of these proliferated seeds have been observed but, as in the normal ones, a single particularly well-preserved specimen was selected for detailed consideration. However, casual study of the other less well-preserved ones clearly indicates that we are dealing with a typical specimen. In view of the unique nature of the fossils the reader is referred to figs. 18 and 19 as an aid in following the description. These are representative peels taken from specimen No. 519.

The over-all dimensions as illustrated in fig. 19 are 13×10 mm. Extending about half way around the specimen (the lower half as it is oriented in figs. 18 and 19) is an epidermis of heavily thickened palisade-like cells which, allowing for some variation among the individuals, agree exactly in size and shape with those of the epidermis of the normal seeds. Within this epidermis there is a parenchymatous tissue which composes the remainder of the fossil. This tissue consists of rather thin-walled cells; it is organically connected with the epidermis; it is vascularized; and it proliferates out into a central area in the form of branches of varying size. Each of these branches contains a delicate vascular strand and is bordered by a well-defined, thin-walled epidermis (fig. 13) which is consequently quite different from the outer epidermis of the fossil as a whole.

It does not seem necessary to comment on the outer thick-walled epidermal layer but a more detailed consideration of the parenchymatous tissue within is very much in order. This consists of rather irregularly shaped cells (fig. 3) in the peripheral region although in the central proliferating arms of tissue (fig. 13) the cells show some tendency to be elongated parallel to the long axis of the arms. It may be noted also in fig. 13 that the epidermis is only slightly differentiated from the interior parenchyma.

It is pertinent to indicate at this point the reasons for correlating these fossils with the previously described normal seeds. The former are, as noted above, somewhat larger and the epidermal layer is split and does not include the entire structure which would be expected if the normal seeds "germinated" to produce the distinctive proliferations shown in figs. 18 and 19. To me, it would seem most likely that the normal seeds or sporangia opened longitudinally along the ridged lateral edges. However, it has not been possible to determine the mechanics of germination from the available specimens, and I find it difficult to glean satisfactory information from Darrah's brief description of this point.

Like the epidermis in the two supposed growth forms, the outer parenchyma of the normal seeds agrees precisely with that of the proliferated seeds. It is clear that the parenchyma is in organic connection with the epidermis just as the epidermis and outer parenchyma of the normal seeds are organically connected, and it is equally clear, as shown in figs. 18 and 19, that there is no break in this parenchymatous tissue from the epidermis to the inner extremity of the arms. The

latter vary considerably in size, some being apparently simple unbranched structures while others branch rather profusely. In the specimen shown in figs. 18 and 19 there may be noted a rather massive central "clump" which gives rise to numerous branches. It will also be noted that many branches appear unconnected with the peripheral tissue but in following the series of peels many of these are readily observed to be connected and I believe that in view of the very close similarity of all of these central islands of tissue (as they appear in an individual peel) there is no reason to doubt that all are so connected. Finally it is important to note that all of these arms are vascularized by a delicate central strand of tracheids similar to those composing the traces of the normal seeds. Although the vascular strands of these are small and composed of few tracheids (fig. 14) the system as a whole is rather extensive. In fig. 18 a tracheidal strand may be noted at *t* and from this lateral strands branch out into the central arms.

Discussion.—

In the opening paragraph of his recent contribution Darrah states that "The discovery of well-preserved fossil embryos in a known plant group is therefore an event of considerable interest." There can be no doubt that such a discovery would be enthusiastically welcomed by botanists in general and paleobotanists in particular, and it is one that may be expected with justification due to the present interest in the coal-ball petrifications. It is, however, my belief that satisfactory proof of this discovery has not been offered to date. It is not a pleasant task to have to refute the work of a colleague but in view of the seeming importance of these fossils no other course seems feasible. It is very possible that the restorations presented in Darrah's figs. 14-17 and fig. 45 (1949) might well be taken up by writers of text-books and without a first hand knowledge of the fossils it must be admitted that his descriptions are fairly convincing. It is my contention that these restorations showing "Lepidodendroid embryos" within the sporangia are entirely unjustified from the anatomical evidence, that the succession of tissues contained within the fossils has been misinterpreted, and that the evidence does not support the view that they are of lycopod affinities.

I wish to admit freely that satisfactory conclusions regarding the natural relationships of this fossil have not been reached yet. For nearly three years I have pondered over their morphology and affinities and have discussed them with numerous paleobotanists and morphologists. Sincere thanks are due to many of my colleagues for consoling suggestions. These fossils remain as the most problematical ones that I have had occasion to study, but in view of the above-mentioned publications it seemed necessary to present the results of my own observations to date. If future investigations are able to improve on the admittedly vague suggestions offered here they will be received cheerfully.

Darrah (1949) has interpreted the conspicuous peripheral parenchymatous tissue as a gametophyte and certain of the central patches of tissue as portions of

an embryo sporophyte. The basis for his differentiation of sporangial wall (or nucellar) tissue from gametophyte is not apparent in his illustrations or from his description. On page 3 he notes: "Close examination shows that a gametophyte has developed within the megasporangium rupturing it and pressing it against the compressed sterile sporangial tissue (remnants of the megasporangium membrane can in nearly all cases, be recognized)." And he also notes on this page that "The gametophyte is relatively undifferentiated." And on later pages reference is made to the "more or less disintegrated" gametophyte in more mature specimens in which the embryo sporophyte has developed at the expense of the nucellus and gametophyte.

Thus there is an essential conflict in our descriptions because my sections show clearly that the "gametophyte" and "nucellar" tissues are continuous and the same. Furthermore, no remnants of the megasporangium membrane can be defined in any of the proliferated seeds I have examined.

In the well preserved specimen which serves as the basis for the present description there is no evidence of any disorganization of tissue in the peripheral region of the parenchyma adjacent to the epidermis. On the contrary, these two tissues are, as noted above, clearly in organic connection. The general organization and degree of maturity appear to be essentially identical with those described by Darrah. It will be helpful in this respect to compare figs. 18 and 19 with Darrah's figs. 3 and 4.

It would seem, therefore, that there is no justification for referring to a tissue organically connected with the epidermis of a sporangium as gametophyte and sporophyte. I can find no evidence for its alleged development within a megasporangium wall. From the prominence of the yellow membrane in the normal seeds there is little question that it would be visible if it were present. It seems especially significant to note that in my specimen the peripheral tissue, that would be termed gametophyte in accordance with Darrah's interpretation, is clearly vascularized. There is no mention of such vascularization in his description, and this oversight may be, in part, responsible for the confusion.

In his fig. 6 Darrah shows what is claimed to be a megasporangium membrane in the lower half of his seed and adds that "the tissue outside being in large part, if not entirely, sterile sporogenous tissue." (p. 7). This is a very critical point, and if it is "not entirely, sterile sporogenous tissue" (presumably this means tissue of the sporangium wall) some explanation of what it might be is certainly in order. In view of my own observations there also is doubt regarding the presence of a megasporangium membrane in the section Darrah has illustrated. The definition of detail in Darrah's fig. 6 is so inadequate that the reader is afforded no basis for reliable interpretation, and the illustration in no way lends objective support to his conclusions.

Perhaps the most serious criticism that I find necessary to make is one pertaining to the reconstruction (fig. 45) of what is apparently a seed containing a

mature embryo. On page 7 Darrah notes four qualifications relative to this reconstruction. It is stated:

1. That the gametophyte is not shown since it would be more or less disintegrated. Yet no specimen is described in which this stage of development is in any way discernible.

2. That "the sporangium, with an embryo of this degree of development, would be ruptured, probably with the embryonic shoot considerably exserted." But the embryo is shown neatly curled within the unbroken sporangium epidermis.

3. That the "embryo would have a much greater number of leaves, particularly at the growing tip." But the description and illustrations in no way bear this out; and if there were many more leaves present it would seem that this point could have been readily shown in the drawing.

4. That "the orientation of the embryo is variable." I certainly agree that these parenchymatous proliferations are variable but it seems equally evident that they do not represent an embryo.

Following the enumeration of these four qualifications he concludes: "Nevertheless this sketch shows the zones of the embryo in their proper relation, and despite the rather unnatural aspect portrays the characteristics faithfully."

Accurate or even tentative paleobotanical restorations are certainly very much to be desired. Mr. Darrah deserves commendation for taking the trouble to summarize his findings in this form so that those who are not familiar with these fossils may gain a clearer concept of their life form, but to contend that the restoration "portrays the characteristics faithfully" seems to be very much at variance with the observable facts.

We may now return to the normal seeds to consider the supposed correlation of their contained tissues with those of the proliferated seeds. It is probably apparent that the most critical phase of this correlation lies in a determination of the origin of the parenchymatous tissue of the proliferated seeds. If Darrah's contentions are correct one would expect to find some remnants of the sporangial wall (nucellus) tissue, the megasporangium membrane, and the gametophyte in those specimens containing immature embryos or even embryos in a rather advanced stage of development. Since no such sequence of disintegrated tissues is in evidence, and since tissues of the supposed gametophyte and sporeling are continuously traceable and connect with the sporangium wall epidermis, some other solution is necessary.

At this point it is pertinent to refer to the inner sclerotic layer of the normal seeds which is shown in figs. 12, 16, and 17. If Darrah's concepts are correct it is hardly possible that this tissue would have been completely disintegrated, yet he makes no mention of it in the germinating seeds. It is not clearly described in his 1941 paper (page 98) but the characteristic sclerenchyma is evident in the top figure of his plate II. No mention is made of the three dimensional aspect and pitting of these cells, so different from any other tissue in either the proliferated or normal seeds. My own observations on the elongate nature and pitting of these

1949]

cells were made largely on Darrah's own slides (preserved in the collections of the Harvard Botanical Museum) and it is difficult to understand why it is not given more prominence at least in the specific description, in view of the fact that, like the vascular strands, it is a tissue quite foreign to *Lepidocarpon*.

In his original paper (1941) on *L. glabrum*, following his discussion of the sporangium wall, Darrah notes that within this "The seed megasporangium is always present" and in a later sentence adds "The gametophyte is extensive, nearly filling the whole cavity." No further description of the gametophyte is given nor do I find it possible to understand the caption to the lower figure of plate II (1941) in which the gametophyte is said to be present. One might overlook this lack on the assumption that the 1941 paper was a preliminary account but I do not feel that his description of the so-called gametophyte in the 1949 paper can be correlated with its organization as presented in the earlier contribution.

In view of the supplementary factual evidence presented here, the divergent descriptions, based, in part, on the same material, and the conclusion that this fossil cannot be referred to the genus *Lepidocarpon* the following emended diagnosis is given:

Nucellangium glabrum (Darrah) emend. Andrews.

Ovoid seed-like bodies approximately 12 mm. long and 6×9.5 mm. in diameter with a small circular hilum scar at proximal end. Presumably a sporangium with a wall consisting of the following sequence of tissues: a thick-walled, columnar epidermis; broad parenchymatous tissue of isodiametric cells; semi-sclerotic, longitudinally elongate, pitted cells; and a narrow thin-walled inner parenchyma. A single large megasporangium contained within. Outer parenchyma traversed from base to apex by two delicate vascular strands.

The supposed proliferated form of the fossil somewhat larger, split longitudinally, consisting of the epidermis and outer parenchyma, the latter with numerous proliferating arms that extend approximately into the former area of the central cavity; peripheral region of this parenchyma as well as arms are vascularized.

Locality: Urbandale coal mine, Des Moines, Iowa, and other localities as given by W. C. Darrah, 1941.

Age: Middle Pennsylvanian, Des Moines series.

Specimens on which the present emended description is based are No. 677 and No. 519 in the paleobotanical collections of the Henry Shaw School of Botany.

In the previous accounts no specimens are specifically designated as the type or types. I have, therefore selected the following from Darrah's papers (1941, 1949) for this purpose: As the type for the normal seeds the specimen illustrated in the top figure of plate II (1941), No. 44103 in the collections of the Harvard Botanical Museum. As the type for the proliferated seeds the specimen illustrated in fig. 2 (1949).

Affinities of the fossil.—

I am keenly aware that the following remarks are inadequate as an explanation of the morphology and affinities of this fossil. It is quite evidently an instance in

which it is easier to destroy than to build, and if too much of the former has appeared in the preceding pages at the expense of a constructive treatment it is due partly to a lack of sufficient information and partly to an admittedly inadequate interpretation.

The suggestions that are given below are based, first, on the belief that *Nucellangium* is not a lycopod. At the expense of repetition the reasons for this belief may be briefly reviewed: The complex sporangium wall with its internal "sclerotic" conducting tissue, the vascularization, and the circular hilum scar. These seem to be of fundamental importance and are not in accord with previously described species of *Lepidocarpon*.

Upon the suggestions of at least two competent morphologists, which, incidentally, were offered independently, the possibility has been entertained that *Nucellangium* represents a hydropterid sporocarp. This possibility was supported by the general shape of the fossils, which is not unlike that of a *Marsilea* sporocarp, the mode of attachment, the thick-walled epidermal layer, and the vascularization of the peripheral parenchymatous tissue. However, certain features of the wall of the normal seeds, notably the inner sclerotic tissue and the single large megaspore, are not in accord with such a relationship, and the fertile specimens show no evidence of having borne sporangia after the manner of *Marsilea*. Furthermore, no associated remains are known which present hydropterid affinities. The possibility of such an affinity has, therefore, been abandoned.

Of the pteridophytic groups, other than the lycopods, which are known from the Upper Carboniferous there seem to be none which present a likely comparison. The remaining alternatives are the pteridosperms or cordaites as seed plant groups, or the possibility that we are dealing with an entirely distinct group of fossils, the affinities of which cannot be conjectured. Since the rest of the plant is not known, speculation in the latter direction at present seems useless. For reasons which will be given below it is, therefore, tentatively proposed that *Nucellangium* be considered as a primitive cordaites seed, or, if more noncommittal terminology seems preferable, a cordaites reproductive organ.

In searching for a lead that might suggest relationships with previously described fossils comparisons have been made with some of the many seed compressions. Of these, certain species assigned to the genus *Cardiocarpus* offer at least provocative suggestions. In examining the specimens of *Cardiocarpus* in the Lacoe Collection of the U. S. Geological Survey a few have been noted which correspond very closely to the expected appearance of a compression specimen of *Nucellangium*. For example *Cardiocarpus minor* Newberry (Lacoe coll., U. S. National Museum No. 25421) presents an aspect virtually identical with the profile of the broad face of the *Nucellangium* fossils. A compression of the latter would almost certainly produce a fossil that would be difficult or impossible to distinguish from this species of *Cardiocarpus*.

Although it is somewhat larger, *Cardiocarpus injens* Lesquereux (Lacoe coll., U. S. N. M. No. 25425) may also be mentioned since it displays an epidermal con-

figuration that compares closely with the type of epidermis of *Nucellangium*. *Cardiocarpus bicuspis* (Sternberg) Lesquereux, another compression species, also is closely comparable in size and shape with *Nucellangium*.

Since it may have some bearing on the present problem it seems significant to note that the many species assigned to *Cardiocarpus* (approximately 125 species are recorded in the U. S. Geological Survey's Compendium Index of Paleobotany) present an amazing variety of form. Were they better known I believe it is conservative to estimate that a few dozens of natural genera are included in this "compression dumping ground." For want of the necessary anatomical information that might allow a different disposition, these fossils are regarded as "seeds" and at present it seems most plausible that they have their alliance with plants of cordaitean affinities.

In tentatively considering the identity of *Nucellangium* with a species of *Cardiocarpus*, such as *C. minor*, a suggestion of the way in which they may have been borne is presented in Lesquereux's figure of *Cordaitanbus spicatus* in the "Coal Flora" (Lesquereux, 1884, III, Pl. 109, fig. 1). Here are seeds of the *Cardiocarpus* type arranged pinnately in two rows on an elongate axis 5 mm. broad. A comparable organization is illustrated by Renault and Zeiller in their 'Flora of Com-
mentry' (Renault and Zeiller, 1888) in figs. 30 and 31 of plate 73. Other authors have figured similar Cordaitalean inflorescences showing seeds of the *Cardiocarpus* type borne apparently terminally on the appendages of short branches. At this point it is perhaps significant to note that the most abundant plant remains in the coal balls from which *Nucellangium* has been obtained are the inflorescences, stems, and leaves of the cordaitales. I am aware that the evidence afforded by association is hardly conclusive, yet in view of the abundance of these cordaitean remains, and the *Nucellangium* fossils which compare closely with compressions known to have been borne on *Cordaitanbus* inflorescences, some significance may be attached to this association.

In attempting to postulate a satisfactory explanation of the morphology and affinities of *Nucellangium* it is clear that the unintegumented nature of the fossil is particularly perplexing. I feel quite certain that the normal seeds as described in the earlier portion of this paper represent a nucellus or sporangium wall and in this one respect I seem to be in accord with Mr. Darrah. Is it plausible that we are dealing with an aberrant cordaitean stock whose presence has not been previously suspected? The possibility may exist, of course, as Darrah suggested, that the seeds were shed from their integuments but at present there appears utterly no evidence that would serve even for conjecture.

It is clear that we are dealing with a sporangium possessing a wall that is specialized as a protective device to a very high degree. Certainly the epidermal layer would have served most effectively against the attacks of fungi or small animals and equally well to prevent the loss of water from within. Can it be that we are dealing with a plant in which this protective function of the integument was developed by the sporangium wall, that is, the tissue that would normally have evolved into a nucellus of the more usual type?

With reference to the morphology of the proliferated seeds the problem becomes much more involved. Having discarded the gametophyte-sporeling nature of these bodies some other explanation is clearly in order. It is tentatively suggested that the proliferated specimens could represent either aposporous growths of the outer parenchymatous layer of the nucellus, or a gemma-type reproductive tissue. If any weight can be placed on the suggestion that the proliferations represent an aposporous tissue it would seem likely that archegonia should be found in some abundance, but none have been observed in the specimen described here. It is, moreover, strange that sporelings, as described by Darrah, are so abundant and yet no trace of their earlier stages is present, and only one archegonium has been reported.

The fact that the parenchymatous tissues of the proliferated specimen, both the peripheral region and the internal "arms," are vascularized, is indicative of sporophytic rather than gametophytic tissue. It would seem, therefore, that the most likely function this structure served was as a purely vegetative reproductive organ—that is, a gemma in the broad sense. It is assumed, following this interpretation, that the proliferations developed directly into a new sporophyte plant. Such being the case, it seems likely that the central proliferated "clump" shown in figs. 18 and 19 represents the initial apical meristematic region of the new sporophyte.

The question of course will arise as to the disappearance of the inner sclerotic layer which is so conspicuous in the normal seeds and the only explanation that I am able to offer is that the characteristic development of the proliferated seeds originated before the normal maturation of the internal tissue layers.

Acknowledgment.—

The abundant Urbandale coal balls, containing a wealth of well preserved, unique plants have been gathered by Mr. Frederick O. Thompson of Des Moines. Unfortunately it has not been possible to obtain more of this material in recent years and although we may reasonably hope that other Iowa localities will eventually contribute toward a more satisfactory solution of this and other paleobotanical problems there appears to be little chance of obtaining more Urbandale coal balls. It is partly on this account that the present writer has decided to submit his study of the available specimens of the fossil described above.

It is a pleasure to acknowledge again with gratitude the contributions that Mr. Thompson has made in aid of our investigations of American Carboniferous plants.

Sincere thanks are also due Dr. James M. Schopf for his many helpful suggestions during various stages of this study. The author, however, assumes all responsibility for such criticism, theories, and conclusions as may be found herein.

Bibliography.—

Andrews, H. N. and Jules Kernen (1946). Contributions to our knowledge of American Carboniferous floras. VIII. Another *Medullosa* from Iowa. *Ann. Mo. Bot. Gard.* 33:141-147.
Darrah, W. C. (1941). The fossil flora of Iowa coal balls. IV. *Lepidocarpon*. *Harv. Univ. Bot. Mus. Leaf.* 9:85-100.
_____, (1949). Paleobotanical Notices II. Paleozoic Lepidodendroid embryos. Medford, Mass. published by the author.
Lesquereux, L. (1884). Coal flora of the Carboniferous formation. 2nd Geol. Surv. of Penna.
Renault, B. and R. Zeiller (1888). *Études sur le terrain houiller de Commentry*, Atlas. Soc. del Industr. Min., St. Etienne.
Scott, D. H. (1901). On the structure and affinities of fossil plants from the Palaeozoic rocks. IV. The seed-like fructification of *Lepidocarpon*, a genus of lycopodiaceous cones from the Carboniferous formation. *Phil. Trans. Roy. Soc. Lond.* 194:291-333.

nes
ese
at
he
ue.
an
me
is,
ret
en

th
of
he
ve
re-
ch
gs.

tic
: I
eds

ed,
es.
nt
lly
cal
ls.
dy

fr.
ts.
g-
all
in.

on-
ot.
ass.

del
IV.
on-

EXPLANATION OF PLATE

PLATE 35

NOTE: A considerable number of the following figures are taken from the series of peels described on pages 481-485. The peel number refers to the respective position as indicated in text-fig. 1. The slide number is the permanent one assigned in the paleobotanical slide collection of the Henry Shaw School of Botany.

Nucellangium glabrum

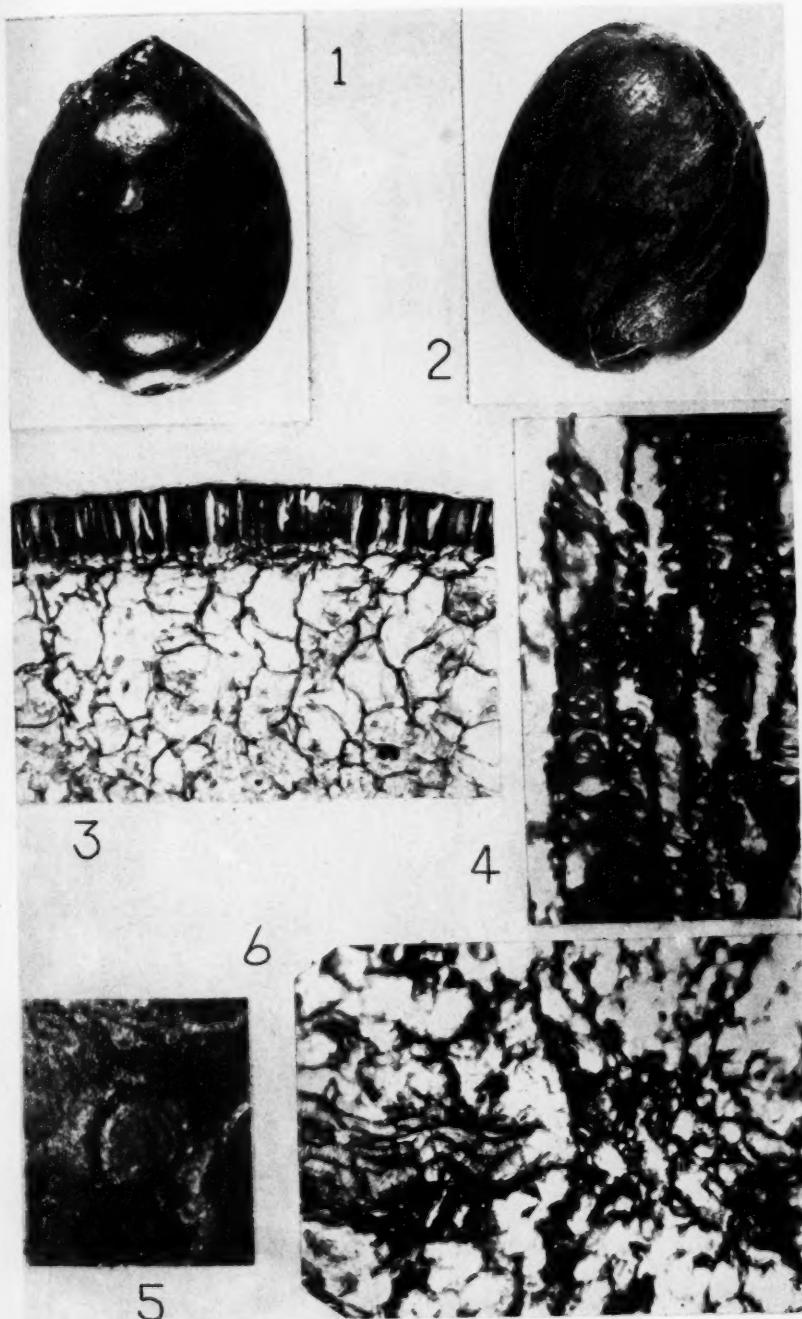
Figs. 1, 2. Specimens isolated whole from coal balls. The one in fig. 1 displays the hilum scar at the base; this specimen was used in preparing the series of peels described on pages 481-485. $\times 5$.

Fig. 3. Epidermis and outer parenchyma showing the two in organic connection in a proliferated seed. Slide No. 1497. $\times 85$.

Fig. 4. Cells, showing pitting, of the inner sclerotic tissue of a sterile seed in longitudinal view. From slide No. 50896, collections of the Botanical Museum of Harvard University. $\times 225$.

Fig. 5. Hilum scar of the specimen shown in fig. 1. $\times 20$.

Fig. 6. Photograph of peel No. 9 (slide No. 1643) showing central vascular strand (near base of seed) in right center, and departing trace at left. $\times 110$.



EXPLANATION OF PLATE

PLATE 36

Nucellangium glabrum

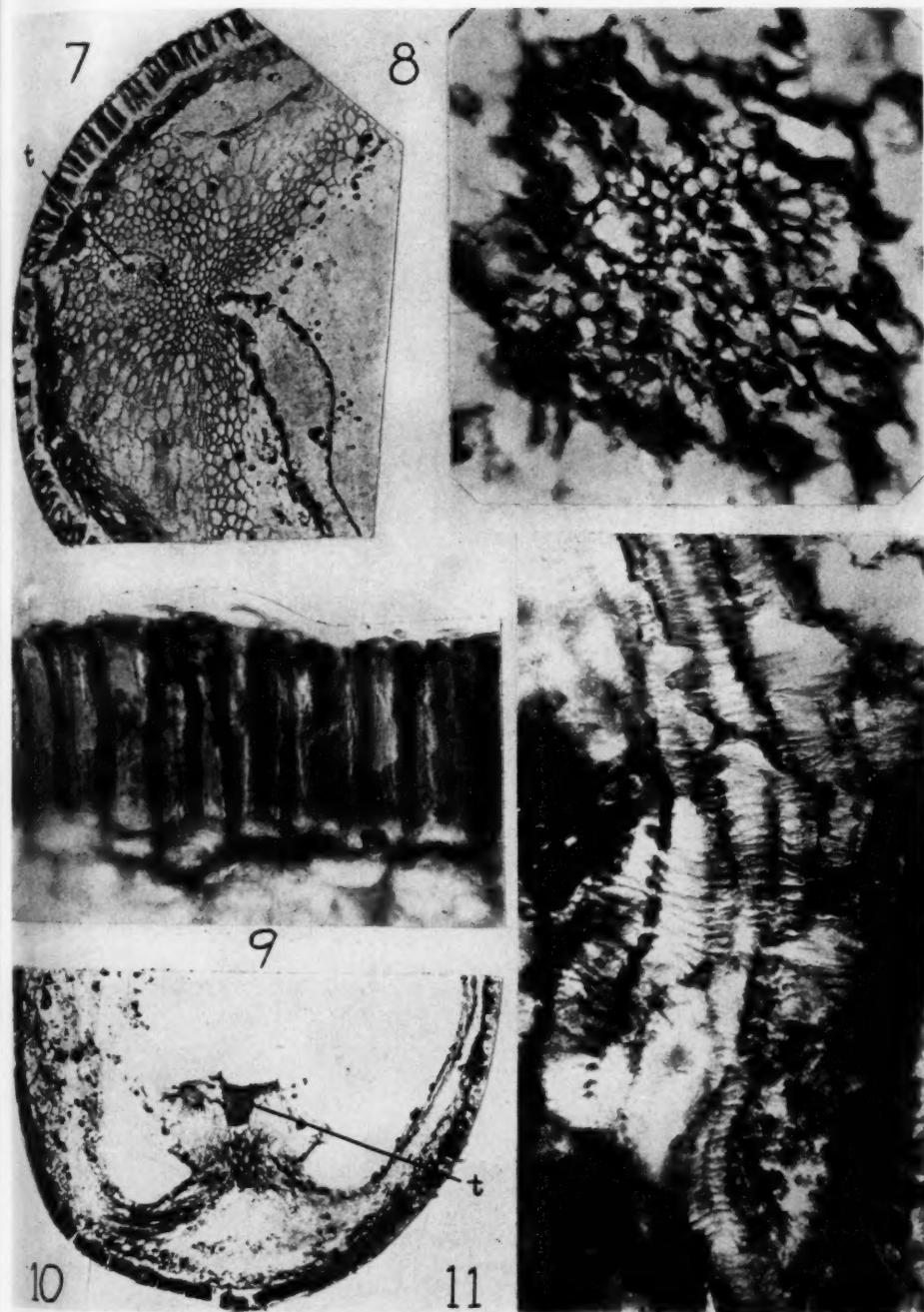
Fig. 7. Part of transverse section through the median region of a seed showing the vascular trace on that side. From slide No. 50897, collections of the Botanical Museum of Harvard University. $\times 54$.

Fig. 8. The central vascular strand in the base of the seed, from peel No. 13 (slide No. 1647). $\times 220$.

Fig. 9. Section through epidermis of normal seed, from peel No. 34 (slide No. 1656). $\times 280$.

Fig. 10. A nearly median longitudinal section through the basal portion of a seed. *t*, tracheidal tissue in "archesporial pad." From slide No. 50895, collections of the Botanical Museum of Harvard University. $\times 16$.

Fig. 11. A highly magnified view of a branch trace of the normal seed, from peel No. 8 (slide No. 1642). $\times 500$.



EXPLANATION OF PLATE

PLATE 37

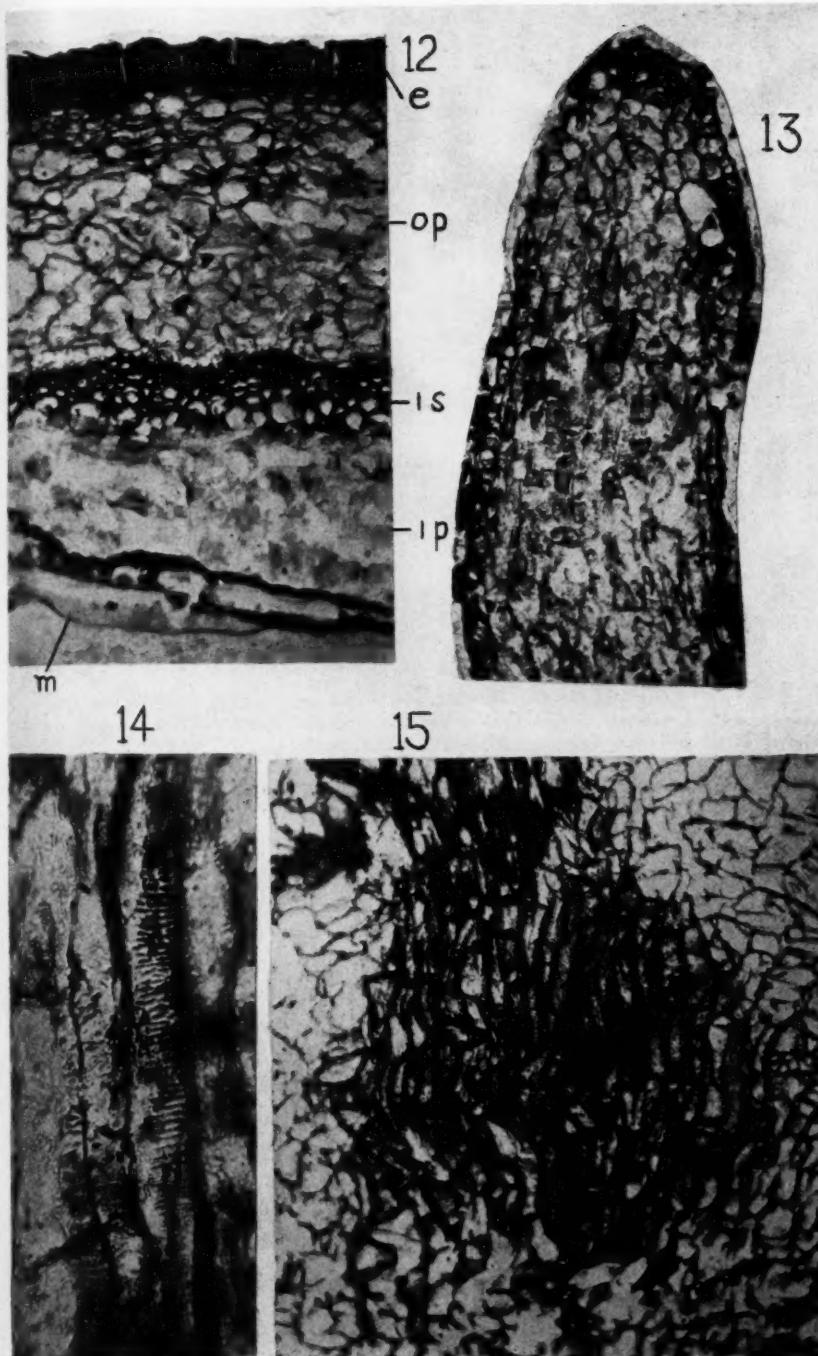
Nucellangium glabrum

Fig. 12. Transverse section through the wall of the normal seed, from peel No. 34 (slide No. 1656): *e*, epidermis; *op*, outer parenchyma; *is*, inner sclerotic layer; *ip*, inner parenchyma; *m*, megasporangium. $\times 65$.

Fig. 13. One of the central arms, or branch proliferations, from the specimen in fig. 18. Slide No. 1496. $\times 80$.

Fig. 14. A vascular strand of the proliferated specimen (fig. 18). Slide No. 1498. $\times 440$.

Fig. 15. A section in the transverse plane through a normal seed taken at one side of the central basal strand. The dark tissue represents the lowermost extension of the inner sclerotic tissue. This is associated at this level with the departing traces and is shown in text-fig. 3 (3) as the small central cross-hatched areas. From peel No. 11 (slide No. 1645). $\times 80$.



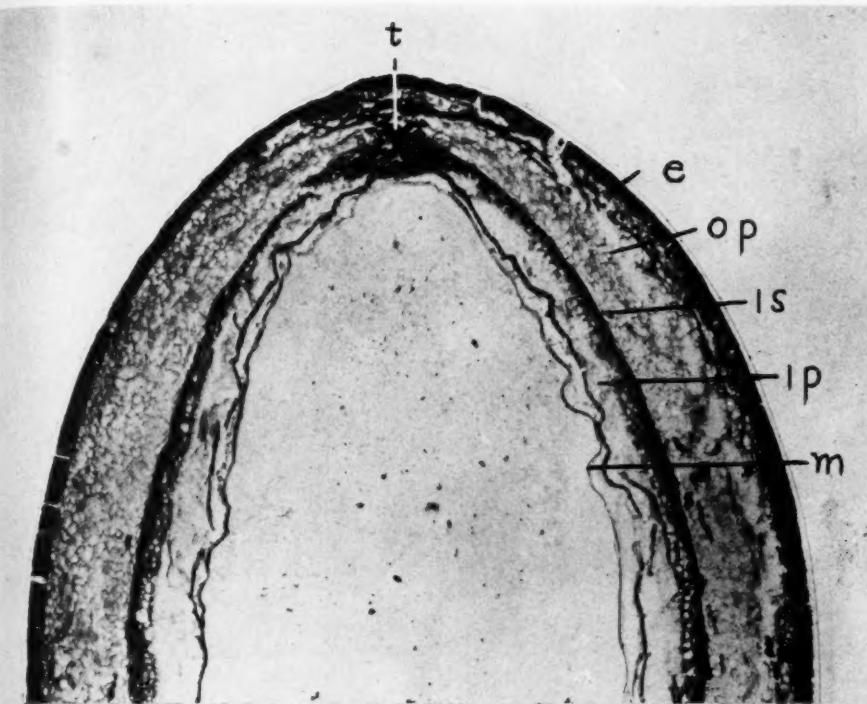
EXPLANATION OF PLATE

PLATE 38

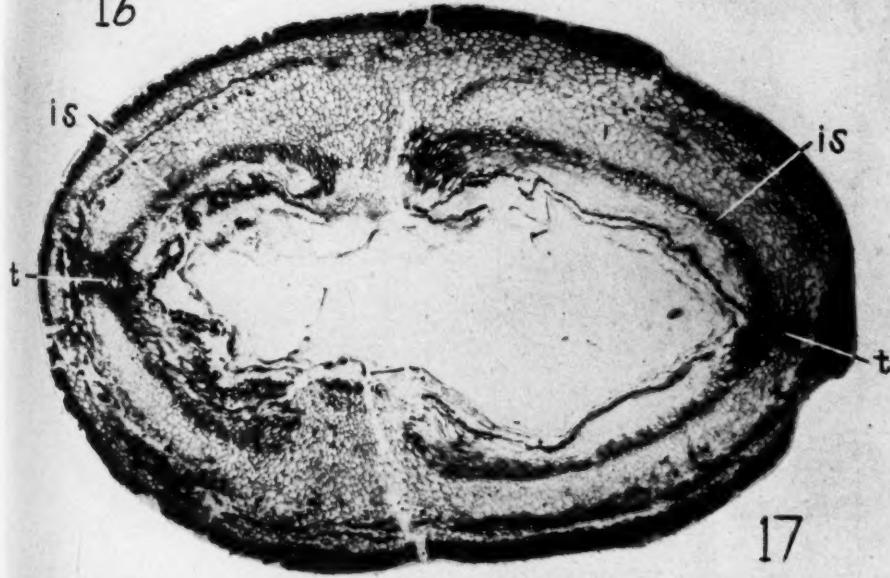
Nucellangium glabrum

Fig. 16. Photograph showing half of the transverse section of the normal seed, peel No. 38 (slide No. 1658): *e*, epidermis; *op*, outer parenchyma; *is*, inner sclerotic layer; *ip*, inner parenchyma; *m*, megaspore membrane; *t*, vascular trace. $\times 20$.

Fig. 17. Complete transverse section of the normal seed, peel No. 20 (slide No. 1653): *t*, position of traces; *is*, inner sclerotic layer. Note interruptions of the inner sclerotic layer on the two sides; compare with text-fig. 3 (4). $\times 18$.



16



17

EXPLANATION OF PLATE

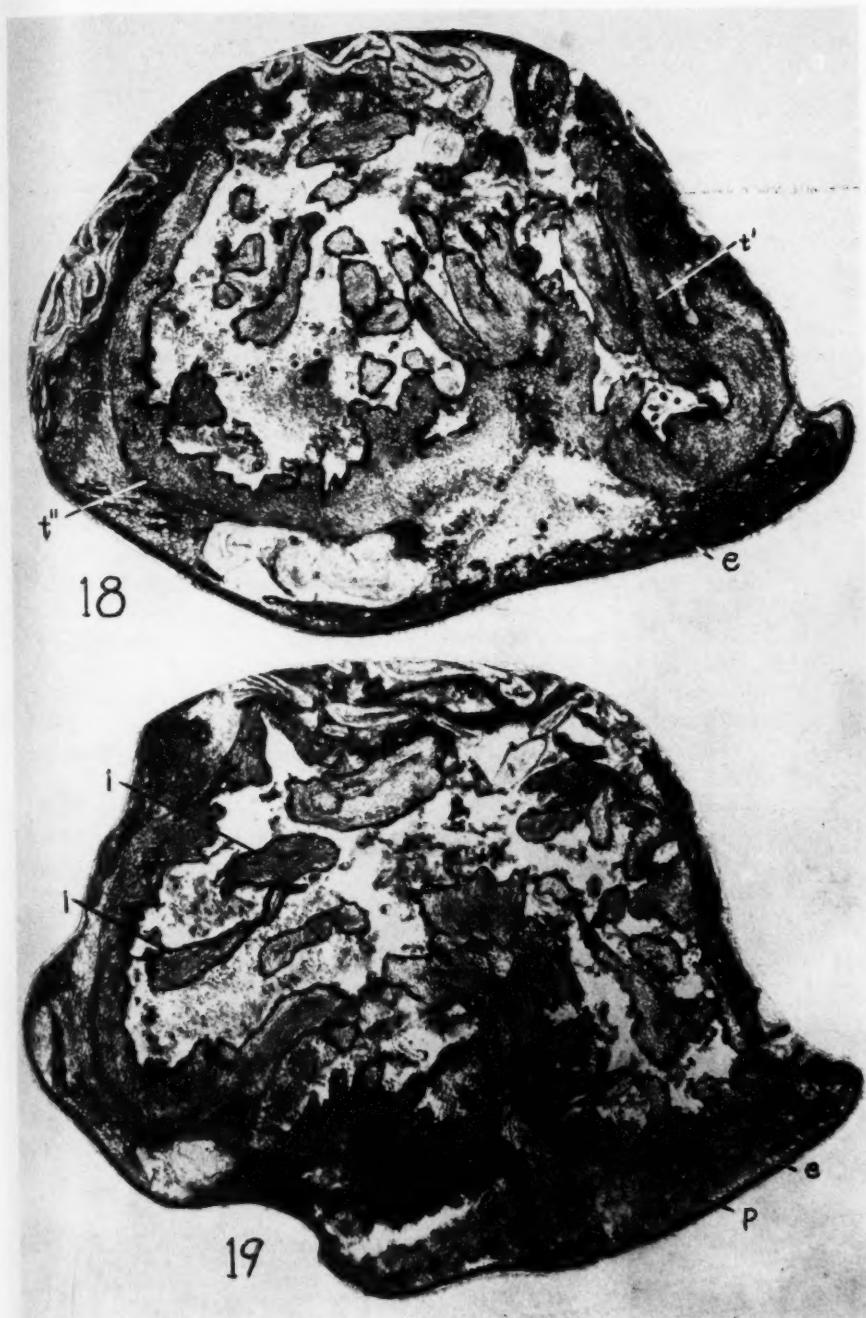
PLATE 39

Nuce'langium glabrum

Figs. 18, 19. Photographs of sections of the proliferated specimen described on pages 486-488.

Fig. 18. From peel No. 519.T7 (slide No. 1674): *t'*, vascular strand in proliferated arm (see fig. 14); *t''*, vascular strand in peripheral parenchymatous zone; *e*, epidermis. $\times 12$.

Fig. 19. From peel No. 519.T29 (slide No. 1675): *e*, epidermis; *p*, peripheral parenchymatous zone which is in organic connection with the epidermis (*e*), and from which the proliferated arms arise; *i*, by following through successive peels these scattered "islands" of tissue may be observed to be proliferated from the peripheral parenchyma zone. $\times 16$.



A REVISION OF THE GENUS HELIOCARPUS L.¹

KO KO LAY

INTRODUCTION

Heliocarpus has received considerable attention from plant systematists probably because of the perplexing variation found in the genus and because of the few constant characters of taxonomic value. Furthermore, in the herbarium, the specimens are either in fruit or in flower, never both; and when in flower are either hermaphrodite or pistillate. Thus, assigning them to any particular species becomes extremely difficult. Despite a recent taxonomic study of the genus,² there is still considerable confusion regarding many species both in the literature and in the herbarium. More than fifty species and varieties have been named thus far, and with the prevalent vagueness in the concept of speciation, there appears superficially to be but two alternatives: either to split the genus into innumerable indistinct and undefinable "species" or to lump them indiscriminately into few categories of scarcely greater reality.

In my study of the genus an attempt has been made to escape this dilemma by clarifying the concept of speciation. However, as this study has been confined entirely to herbarium specimens which represent only very small portions of the woody plants, no definite idea or suggestion as to the individual variations of single plants has been obtained. I have been fortunate enough in being able to study specimens from nearly all the major herbaria both in the United States and in Europe. The standard method of the herbarium taxonomist has been used for the interpretation of the species, and an attempt has been made to identify the fruiting specimens with the flowering ones. As far as possible, no intergrading forms have been considered as worthy of specific rank, and I have tried to group the "species" into fewer categories of perhaps greater biological reality, in the hope that they will be satisfactory both from a taxonomic and from a practical standpoint. The key has been so prepared that it should be usable for both the fruiting and the flowering specimens.

GENERIC RELATIONSHIPS

Heliocarpus L.³ commonly is referred to the tribe *Grewieae*⁴ of the family Tiliaceae and usually is recognized by its characteristic fruits. The genus is distinct from the other genera of *Grewieae* except *Triumfetta*. There is no difficulty in distinguishing the two genera when both are in fruit, as the fruits are very dis-

¹An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Arts in the Henry Shaw School of Botany of Washington University.

²Watson, E. E. The genus *Heliocarpus*. Bull. Torrey Bot. Club 50:109. 1923.

³Sp. Pl. ed. 1. 448. 1753.

⁴K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. III⁶:29. 1895.

tinct. A very good description of the fruit of *Heliocarpus* was given by Linnaeus⁵, who asked, in naming the genus, "Who could ever behold an almost rounded fruit, bordered with a halo of rays, without thinking of the sun as conceived by the painters?" In *Triumfetta* the fruit is a burr, with many bristles all over the surface.

It is slightly more difficult to differentiate between the two genera in the case of flowering specimens. Both have alternate, palmately reticulated leaves with long, slender petioles and stellate pubescence. The aspect of the specimens also is very similar and the superficial resemblance rather striking. The chief differentiating characters may be summarized as follows:

(1) *The inflorescence*—In *Heliocarpus* usually terminal, and when axillary large and spreading; in *Triumfetta* generally axillary, rarely large and spreading.

(2) *The cymes*—In *Heliocarpus* disposed in nodose clusters of about 12–20 flowers each; in *Triumfetta* generally not in nodose clusters, and if in nodose clusters usually 6- to 12-flowered.

(3) *The flowering peduncles*—In *Heliocarpus* nearly always 3-flowered (rarely 2-flowered), and usually ebracteolate; in *Triumfetta* 1- or 2-flowered (rarely 3-flowered) and conspicuously bracteolate.

(4) *The mature floral buds*—In *Heliocarpus* as long as 6–7 mm., the sepals appendaged or unappendaged at the tips, the petals valvate; in *Triumfetta* as long as 2–3 cm., the sepals always with apical appendages, the petals with twisted aestivation.

(5) *The number of stamens*—In *Heliocarpus* usually 12–40; in *Triumfetta* usually more numerous.

(6) *The gonophore*—Simple in *Heliocarpus*; in *Triumfetta* with a ciliate saucer-shaped margin (urceolus) surrounding the stamens.

(7) *The ovary*—In *Heliocarpus* either borne upon a gynophore or sessile upon the gonophore, 2-celled, laterally compressed and ciliate about the margins; in *Triumfetta* always sessile upon the gonophore, 3- to 5-celled, not laterally compressed, and generally pubescent.

(8) *The style*—In *Heliocarpus* not more than three to four times the length of the ovary, usually much shorter, always bifid at the tip with the stigma lobes spreading; in *Triumfetta* usually longer than three to four times the length of the ovary, simple throughout, the stigma flattened or capitate.

Heliocarpus can be divided into two major groups of species based on the presence or absence of a gynophore in flower or fruit; further, the presence of appendages at the tips of the sepals is a character which is correlated in the majority of species (except in *H. mexicanus* and *H. nodiflorus*) with the absence of the gynophore.

⁵Critica Botanica (transl. by Hort and Green). Roy. Society, London. p. 79. 1938.

GEOGRAPHICAL DISTRIBUTION

The geographical range of *Heliocarpus* embraces nearly the whole of the tropical Americas. With the exception of the predominantly South American *H. popayanensis*, the species are indigenous entirely to Mexico and Central America. The presence of some plants of *H. popayanensis* in Hawaii apparently is due to recent introduction for reforestation in the foothills. Possibly in the same category is the presence of some plants of *H. Donnell-Smithii* in Martinique.

The species can be divided into five groups with respect to their geographical distributions:

- (1) Northwestern Mexico—*H. attenuatus* and *H. Palmeri*.
- (2) Southwestern Mexico—*H. terebinthinaceus*, *H. pallidus*, and *H. occidentalis*.
- (3) South-central Mexico and Central America—*H. mexicanus*, *H. appendiculatus*, *H. Donnell-Smithii*, and *H. nodiflorus*.
- (4) Southeastern Mexico—*H. americanus*.
- (5) Southern Central America and South America—*H. popayanensis*.

The species of the sessile-fruited group are confined for the most part to the northern range of the distribution; while those of the stipitate-fruited group, where the fruits are borne upon bristly gynophores, are mostly in the middle and southern areas of distribution.

The northernmost limit of the genus is in subtropical Sonora and Chihuahua, Mexico, where the plants grow in canyon forests or oak flats; the southernmost limit is in central Argentina, where lower elevations along river banks are inhabited.

Except for shrubby plants (*H. occidentalis* and *H. pallidus*), which sometimes grow on barren hill slopes, the majority of the species, consisting of small trees, grow only in moist places at higher elevations, usually at about 1000 m. or more, in rain- or cloud-forests, along roadways or river banks in sheltered places, or on edges of forests (usually on cut-over lands in second growth, where they sometimes form a pure stand).

ECONOMIC VALUE

In so far as is known from collectors' notes and from the published accounts of Standley⁶ and Martinez⁷, the economic importance of *Heliocarpus* is primarily in its bark, which produces a very strong and durable fibre. The bark of the young branches yields a fibre from which a strong but coarse rope is made. It is used also for weaving mats and baskets. The principal component of the Mexican fabric *belem* is the cordage extracted from the barks. Resistant paper formerly was made from the wood in Mexico; in Brazil it is still so used to some extent. The wood of the trees is soft and light and is used for floats and bottle-stoppers. Because of its lightness it has been used for rafts. The bark is used for *mecates* in Guate-

⁶Contr. U. S. Nat. Herb. 23:739. 1923.

⁷Plantas utiles de Mexico, p. 253. 1936.

mala, and a decoction is used in sickness of cattle, and sometimes is applied on sores. In Hawaii the trees have been planted on the foothills for reforestation.

VERNACULAR NAMES

H. americanus: *janote* (Vera Cruz).

H. appendiculatus: *burio*, *burio blanco*, and *burio colorado* (Costa Rica); *cajeton* (Guatemala); *balsa* and *pastano mula* (Nicaragua); *calagua* (El Salvador); *jonote*, *jonote blanco*, *jonote colorado* (Vera Cruz); *majao* (Honduras).

H. attenuatus: *samo baboso* (Sinaloa).

H. Donnell-Smithii: *kolol* (Quintana Roo); *jolocin* (Tabasco); *jonote* (Vera Cruz); *majao* (Honduras); *mobo*, "broad-leaved *mobo*", and "mountain *mobo*" (British Honduras).

H. mexicanus: *antigua*, *cajeto*, and *majagua* (Guatemala); *mobo* (British Honduras).

H. nodiflorus: "broad-leaf *mobo*" (British Honduras); *cajeto* (Guatemala); *majao* (Honduras).

H. occidentalis: *pulmonilla*, *guasima*, and *panigua* (Chiapas and Jalisco).

H. pallidus: *guasima* and *tilia* (Guerrero, Jalisco, and Mexico).

H. Palmeri: *coche* (Sinaloa); *rama kowusamo*, and *palo chinu* (Sonora).

H. popayanensis: *balsa* (Colombia); *majagua* (Venezuela); *palo de balsa* (Peru); *sanpan* (Ecuador).

H. terebinthinaceus: *cuabualagua* or *quaubalagua* (Morelos and Puebla); *guasima*, *jolotzin*, *majorhua*, and *jonote* (Morelos, Oaxaca, and Guerrero).

ACKNOWLEDGMENTS

During the course of this study, materials from the following herbaria have been examined, for which I wish to acknowledge my indebtedness:

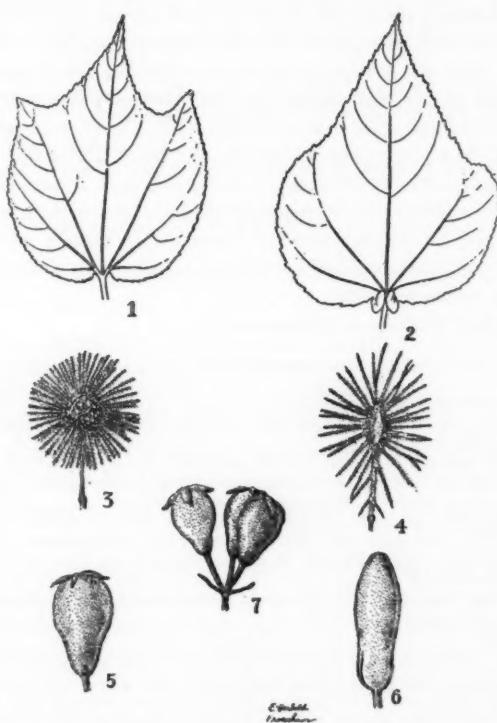
Jardin Principal de l'Etat, Bruxelles, Belgium.
Conservatoire Botanique, Genève, Switzerland.
Chicago Natural History Museum (Field), Chicago, Illinois.
Gray Herbarium of Harvard University, Cambridge, Massachusetts.
Royal Botanic Gardens, Kew, England.
Missouri Botanical Garden, St. Louis, Missouri.
New York Botanical Garden, New York, N. Y.
Royal Botanic Gardens of Trinidad and Tobago, Port-of-Spain, Trinidad, B.W.I.
University of California, Berkeley, California.
University of Michigan, Ann Arbor, Michigan.
United States National Herbarium, Washington, D. C.
I am greatly indebted to the Missouri Botanical Garden and to its director, Dr. G. T. Moore, for the use of its library and herbarium facilities during the course of this study. Particular thanks are due to Dr. R. E. Woodson, Jr., for his advice, guidance, and constructive criticism.

TAXONOMY

HELIOCARPUS L. Sp. Pl. ed. 1. 448. 1753; Gen. Pl. ed. 5. n. 606. 1754.

Adenodiscus Turcz. in Bull. Soc. Nat. Moscou 19²:504. 1846.

Woody trees or shrubs; older branches cream to brown, nearly glabrate, the younger branches usually stellate-pubescent, dark brown, fibrous, with many mucilage canals. Leaves alternate, petiolate, stipulate, the stipules usually large, early deciduous, very rarely persistent, the blade 3-lobed to undivided, venation palmate and either 5- to 7-costate or 3-costate at the base, irregularly serrated, the basal serrations usually glandular, slightly to densely stellate-pubescent, acute to



Illustrations of taxonomic criteria of the genus *Heliocarpus*: 1, leaf of *H. terebinthinaceus* showing the 3-costate venation at the base; 2, leaf of *H. appendiculatus* showing the 3-costate venation at the base and the 2 leafy auricles at the basal sinus; 3, sessile fruit of *H. occidentalis* showing the separate tufts of stellate hairs; 4, stipitate fruit of *H. Donnell-Smithii* borne on a bristly gynophore; 5, floral bud of *H. Palmeri* showing the relatively large, reflexed, trigonal appendages on the tips of the sepals; 6, floral bud of *H. appendiculatus* (note the absence of apical appendages); fig. 7, 3-radiate flowering peduncle (cymule) of *H. Palmeri* with a pair of bracteoles.

acuminate, the base rounded or cordate. Inflorescence gynodioecious or hermaphrodite, usually terminal (axillary in some species), large and spreading, consisting of numerous aggregate dichasia, the main axis branching sympodially and at each node bearing a cluster (cyme) of some 12–20 flowers, the terminal branches with 5–7 cymes, usually more or less secund, each cyme consisting of reduced sympodially branched axes terminating in 3- (rarely 2-) flowered cymules. Flowers either hermaphrodite or pistillate, regular, hypogynous, 4- to 5-merous; the sepals valvate, usually stellate-pubescent without, glabrate within, sometimes with small appendages at the tips; the petals 4–5 in hermaphrodite flowers, absent in the pistillate, free, valvate, 1- to 3-nerved, shorter than the sepals, usually ciliate at the base, sometimes slightly so at the apex; the stamens 12–40 in hermaphrodite flowers, staminodial or absent in the pistillates, borne cyclically on the enlarged gonophore, with 2-lobed, 4-celled, introrse, longitudinally dehiscent anthers; the ovary wholly superior, sessile upon the gonophore or with a manifest gynophore, ellipsoid to orbicular, laterally compressed, ciliate and with shorter pubescence on the faces, 2-celled, falsely 4-celled at the base, each cell with 2 anatropous ovules, the style filiform, bifid at the tip with the stigma lobes spreading and simple or slightly 3-lobed. Fruit dry, indehiscent, 2-celled, 2-seeded, laterally compressed, ellipsoid to orbicular, slightly rugose, sessile or stipitate upon the accrescent gynophore, ciliate with 2 rows of plumose bristles decurrent upon the gynophore when present, the faces pubescent to glabrate; the seed compressed-ovoid or -pyriform, with a median funicular groove, endosperm oily.

Standard species: *Helicocarpus americanus* L.

KEY TO THE SPECIES

- A. Fruit sessile; ovary sessile on the gonophore.
- B. Leaves 3-lobed, veins 3-costate at the base; buds with or without appendages at the tips of the sepals.
 - C. Leaves with dense, coarse pubescence on both surfaces, cordate, 3-lobed, about 14 cm. long and 12 cm. wide; buds sometimes with small appendages at the tips of the sepals; fruit spherical, tomentose; southwestern Mexico.....1. *H. terebinthinaceus*
 - C. Leaves with pale, smooth tomentum beneath, glabrate above, the base rounded to slightly cordate, 3-lobed to obscurely so, about 10 cm. long and 8 cm. wide; buds with conspicuous, erect appendages at the tips of the sepals; fruit ovoid, glabrate; southwestern Mexico2. *H. pallidus*
- BB. Leaves not lobed, veins 5- to 7-costate at the base; buds with conspicuous appendages at the tips of the sepals.
 - C. Leaves cordate.
 - D. Leaves nearly glabrate on both surfaces, about 14 cm. long and 10 cm. wide, acuminate; appendages on the sepals trigonal, large and reflexed; stamens about 40; style about 4 times longer than the ovary; fruit spherical, with a distinct groove in the body, slightly tomentose; northern Mexico.....3. *H. Palmeri*
 - DD. Leaves glabrescent above, tomentose beneath, small, about 8 cm. long and 5 cm. wide, caudate-acuminate; appendages on the sepals linear, erect; stamens 16–20; style about twice the length of the ovary; fruit ellipsoid, tomentose; northern Mexico4. *H. attenuatus*
 - CC. Leaves rounded or cuneate at the base, glabrate or nearly so on both surfaces; appendages on the sepals short, erect; stamens about 40; style about twice the length of the ovary; fruit ovoid with short, separate tufts of stellate hairs; southwestern Mexico.....5. *H. occidentalis*

AA. Fruit borne on a bristly gynophore; ovary borne on a gynophore upon the gonophore.

B. Inflorescences axillary, leafy; leaves not lobed, the base obtuse, glabrate above, slightly tomentose beneath; buds with conspicuous appendages at the tips of the sepals; stamens about 25-30; fruit ellipsoid, glabrous; southern central Mexico and Central America 6. *H. mexicanus*

BB. Inflorescences generally terminal, not leafy.

C. Leaves with two conspicuous auricles at the basal sinus, usually not lobed, the base rounded or subcordate, glabrate above, tomentose beneath; buds without appendages at the tips of the sepals; stamens about 30; fruit suborbicular, tomentose; southern central Mexico and Central America 7. *H. appendiculatus*

CC. Leaves without conspicuous auricles at the basal sinus.

D. Leaves not lobed, rounded at the base, not longer than 14 cm. or wider than 10 cm.

E. Leaves very densely tomentose beneath, glabrate above; stamens about 20; style very briefly bifid; fruit orbicular, tomentose; southeastern Mexico 8. *H. americanus*

EE. Leaves glabrate on both surfaces; stamens about 12-16; style bifid about half its length; fruit ellipsoid, glabrate; southern central Mexico and Central America 9. *H. Donnell-Smithii*

DD. Leaves generally 3-lobed, cordate at the base, about 17 cm. long and over 14 cm. wide.

E. Leaves glabrate above, the lower surface puberulent with short, stellate and long, simple hairs, especially on the veins; buds without appendages at the tips of the sepals; stamens about 12; style briefly bifid, each stigma with 3 acute lobes; fruit ovoid, slightly tomentose to nearly glabrate; southern Central America and South America 10. *H. popayanensis*

EE. Leaves glabrate on both surfaces, veins not pubescent on the lower surface; buds sometimes with short appendages at the tips of the sepals; stamens about 24; style bifid about half its length, stigma-lobes simple, acute; fruit orbicular, slightly tomentose; southern Mexico and Central America 11. *H. nodiflorus*

1. HELIOCARPUS TEREBINTHINACEUS (DC.) Hochr. in Ann. Conserv. et Jard. Bot. Genève 18:125. 1914.

Grewia terebinthinaceus DC. Cat. Hort. Monsp. 114. 1813. (T.: *Berlandier 1064*).
H. Nelsonii Rose, in Contr. U. S. Nat. Herb. 6:128. 1897. (T.: *Nelson 1485*).
H. reticulatus Rose, loc. cit. 128. 1897. (T.: *Pringle 1791*).
H. microcarpus Rose, loc. cit. 8:316. 1905. (T.: *Pringle 8719*).

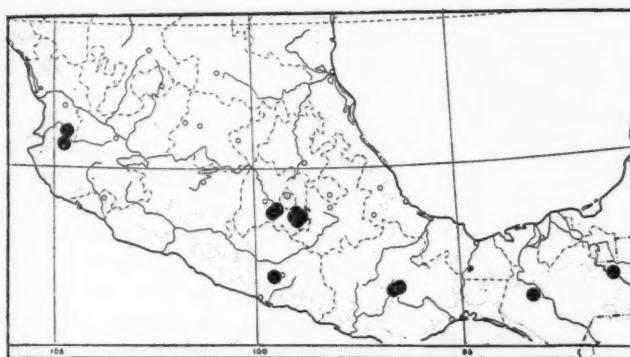
Small trees or shrubs 4-5 m. high; older branches cream to brownish, glabrate, slightly longitudinally ridged, irregularly punctate with white lenticels; younger branches and inflorescence axes rough, scurfy, ferruginous-tomentose with stellate hairs. Leaves 3-lobed, acuminate, about 13-15 cm. long and 10-12 cm. wide, 3-costate, the mid-costa arising independently of the lateral costae, and each lateral costa consisting of 2 or 3 veins united at the basal sinus, base cordate, irregularly and bluntly serrated, both surfaces light green or pale brownish with thick, matted, stellate pubescence, the veins more pubescent with both stellate and long simple hairs; petioles slender, about 8 cm. long, covered with ferruginous tomentum. Inflorescences gynodioecious; the hermaphrodite usually axillary, rarely terminal, large and leafy, usually about 20 cm. long and 15 cm. wide, sometimes about 25 cm. long and 20 cm. wide, the cymes of about 15-18 flowers, rather compact in nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels about 2 mm. long, the buds obovoid, constricted towards the base, sometimes with small erect appendages on the tips of the sepals, the sepals 4, spatulate, about 4-5

Fig. 1. *H. terebinthinaeus*

mm. long, densely stellate-tomentose without, glabrate within, the petals 4, linear, 1-nerved, about 3-4 mm. long, the ovary ellipsoid, about 1.5 mm. long, sessile, with a style about 3 mm. long, bifid about one quarter of its length and with stigma lobes acute, spreading; the pistillate much smaller than the hermaphrodite, about 10-15 cm. long and 8-10 cm. wide, the cymes of about 18 flowers, very much crowded in compact nodose clusters, the flowering peduncles 3-radiate, very short, less than 1 mm. long, the pedicels about 1-2 mm. long, the buds obovoid, not appendaged at the tips of the sepals, the sepals 4, linear, about 2 mm. long, densely stellate-tomentose without, glabrate within, the petals none, the staminodes about 10-12, the ovary ellipsoid, minute, sessile, with a style about twice the length of the ovary, briefly bifid at the tip, and with the stigma lobes acute. Fruit suborbicular, 4-5 mm. in diameter, rather densely tomentose, sessile, the fringe of two rows of plumose bristles about 5-7 mm. long; the seed ovoid, about 2 mm. long, with a very slight groove in the middle.

Distribution: On the highlands of central Mexico, especially on open hill slopes, altitude above 1000 m. Flowers throughout September and October, and fruits from late October to December.

MEXICO: CHIAPAS: Tuxtla Gutiérrez, Juzepczuk 1461. GUERRERO: above Chilpancingo, Nelson 7046; Sierra Madre, alt. 1250 m., Langlassé 572. JALISCO: road to San Domingo mine, alt. 5160 ft., Etzatlán, Barnes & Land 285; barranca, Guadalajara, alt. 4500 ft., Pringle 9693; Guadalajara, Pringle 1791. MEXICO: Tejupilco, Temascaltepec,

Map 1. Distribution of *H. terebinthinaceus*

Hinton 6736; Acatitlan, Temascaltepec, alt. 1130 m., Hinton 5119. MORELOS: Cuernavaca, alt. 5000 ft., Pringle 8227; lava field near Yantepec, alt. 4000 ft., Pringle 9692; vicinity of Cuernavaca, Lemmon & Lemmon s. n.; Cuernavaca, Atlacomulco, alt. 1300–1400 m., Woronow 2333; Cuernavaca, Berlandier 1064; Cuernavaca, Bourgeau 1200; about Cuernavaca, alt. 5000 ft., Pringle 8719. NAYARIT: El Trapiche, s. e. of Yxtian, alt. 1200 m., Mexia 809. OAXACA: Valley of Oaxaca, alt. 5100–5800 ft., Nelson 1243; Valley of Oaxaca, alt. 5500–7500 ft., Nelson 1485; on slopes east of Cincatlan, alt. 2500–4000 ft., Nelson 1818; Rio Blanco, San Juan del Estado, alt. 5000 ft., L. C. Smith 797; Monte Alban, alt. 6200 ft., L. C. Smith 939; Hacienda Guadalupe, alt. 1600 m., Conzatti s. n.; Tomellin Cañon, near city of Oaxaca, Rose & Hough 4565. DATA INCOMPLETE: Ahualulco ?, Barcena, Urbina 639.

This species is very distinct and can be recognized easily by its 3-lobed leaves with the characteristic venation, and also by its sessile fruits. Hochreutiner pointed out that Berlandier 1064, collected from Cuernavaca, which Rose cited for *H. Nelsoni*, is identical with the specimen which de Candolle, on the assumption of a 4-locular ovary, described as *Grewia terebinthinaceus*.

Rose differentiated his *H. Nelsoni* (type: Nelson 1243 & 1485), *H. reticulatus* (type: Pringle 1791) and *H. microcarpus* (type: Pringle 8719) primarily on the degree of pubescence on the fruits. This character is extremely variable. In matching the three types, it is noticeable that *H. microcarpus* has slightly smaller fruits and that the flowers have minute erect appendages. The size of the fruits varies slightly from plant to plant and sometimes on the same plant. Furthermore, the apical appendages on the sepals, when present, are extremely minute and not clearly seen. As they stood, it was difficult to tell the three species apart and there were many misdeterminations.

2. HELIOCARPUS PALLIDUS Rose, in Contr. U. S. Nat. Herb. 5:128. 1897. (T.: E. Palmer 157).

H. velutinus Rose, loc. cit. 8:317. 1905. (T.: Pringle 8694).

Fig. 2. *H. pallidus*

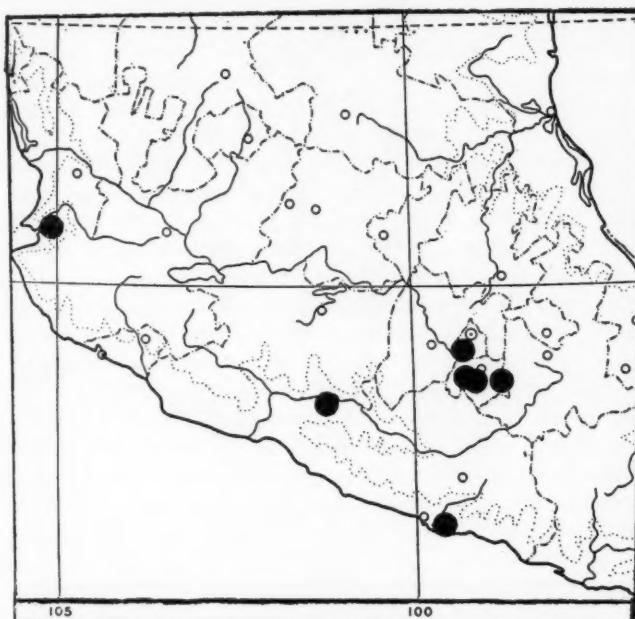
Small trees or shrubs about 2–4 m. high; older branches yellowish brown, glabrate, slightly rugose, punctate with few white lenticels; younger branches and inflorescence axes scurfy, slightly ferruginous-tomentose. Leaves small, younger ones generally not lobed or obscurely so, older ones 3-lobed, about 8–10 cm. long and 7–8 cm. broad, 3-costate, with the midcosta arising independently of the two lateral costae, and each lateral costa consisting of 2 or 3 veins united at the sinus, base usually cordate or subcordate, in younger leaves slightly rounded, acuminate, irregularly serrated, upper surface dark green, glabrate, lower surface whitish, densely stellate-tomentose with appressed hairs; petioles long and slender, 6–7 cm. long. Inflorescence hermaphrodite, usually axillary, large and spreading, leafy, about 14–20 cm. long and 12–20 cm. wide; the cymes of about 12–15 flowers borne loosely in nodose

clusters, the flowering peduncles 3-radiate, about 2–3 cm. long, the pedicels about 4–5 mm. long, the buds obovoid, constricted at the base, with small linear, acute, erect appendages at the tips of the sepals, the sepals 4, linear, 4–6 mm. long, light green and slightly stellate-pubescent without, glabrate and yellowish within, the petals 4, linear, about 3–4 mm. long, the ovary ovoid, small, 0.5–1.0 mm. long, sessile, with a style about twice the length of the ovary, briefly bifid at the tip, and with the stigma lobes acute. Fruit ovoid, usually in compact clusters, very tomentose when immature, becoming glabrate at maturity, about 5 mm. long and 3 mm. wide, sessile, the fringe of two rows of plumose bristles about 4–5 mm. long; the seed obliquely ovoid, about 3 mm. long and 2 mm. wide, with a very deep groove in the middle.

Distribution: On the highlands of central and southwestern Mexico, especially on open hill slopes, altitude above 500 m. Flowers from October to November, and fruits in December and January. Usually leafless in January.

MEXICO: GUERRERO: Paso de las Vacas, Nelson 6970; Pungarabato, Coyuca, Hinton 7243; Acapulco and vicinity, E. Palmer 157. JALISCO: Puerto Vallarta, El Real, Mexia 1100. MEXICO: Chorrera, Temascaltepec, alt. 1350 m., Hinton 5416; Ocotepec, Temascaltepec, Hinton 7036; Tenayac, Temascaltepec, Hinton 5109; Chorrera, Temascaltepec, Hinton 7236; Ixtapan, Temascaltepec, Hinton 7155. MORELOS: near Yantepec, alt. 4500 ft., Pringle 8694; Cuernavaca, Berlandier 971. DATA INCOMPLETE: Haenke 2468.

The types of the two species *H. pallidus* (E. Palmer 157) and *H. velutinus* (Pringle 8694) have leaves which apparently look distinct, those of *H. pallidus* being small, obscurely 3-lobed, with rounded base, and of *H. velutinus* relatively



Map 2. Distribution of *H. pallidus*

small but definitely 3-lobed with subcordate base. It is apparent that the type of *H. pallidus* represents the immature and that of *H. velutinus* the mature state of the leaves. On the same branch (cf. *Hinton 5416* and *Mexia 1100*) the leaves at the base of the specimens may correspond to those of *H. velutinus* and those near the tip to *H. pallidus*.

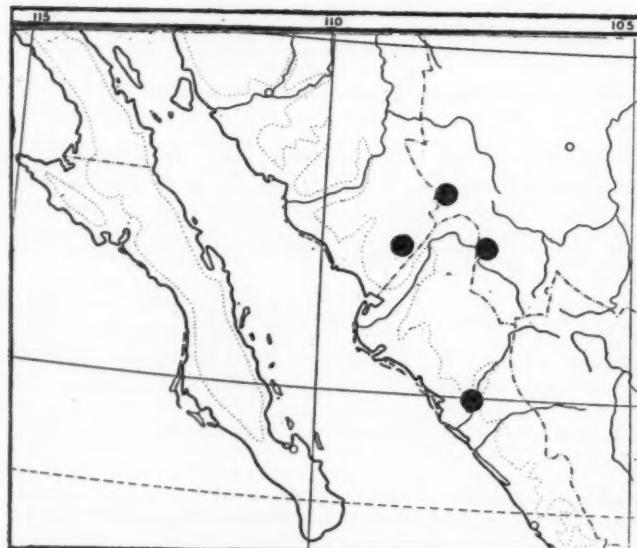
The fruits on the type of *H. velutinus* are slightly larger and more glabrate than those on the type of *H. pallidus*. There are many intermediates between these two extremes, in specimens that answer to the above descriptions. Presumably the fruit, which is slightly tomentose when young, becomes nearly glabrate at maturity.

3. *HELOCARPUS PALMERI* S. Wats. in Proc. Amer. Acad. 21:420. 1886. (T.: *E. Palmer 191*).

H. polyandrus S. Wats. loc. cit. 1886. (T.: *E. Palmer 100*).

H. glaber Brandegee, in Zoe 5:207. 1804. (T.: *Brandegee s. n. in Herb. Calif.*).

Diffusely spreading shrubs about 2-3 m. high; older branches dark brown, glabrate with few short tufts of stellate hairs mostly around the white lenticels; younger branches and inflorescence axes covered lightly with short stellate tomen-

Fig. 3. *H. Palmeri*Map 3. Distribution of *H. Palmeri*

1949]

tum. Leaves broadly ovate, 12–14 cm. long and 8–10 cm. wide, not lobed, 5-costate, narrowly acuminate, base cordate or subcordate, thin, unequally and bluntly serrated, basal serrations glandular, upper surface dark green, nearly glabrous to glabrate, rough, with few short suppressed, scattered tufts of stellate hairs, sometimes slightly scabrous on the veins, lower surface lighter green, slightly more pubescent than the upper, nearly glabrate, generally coarse, with short suppressed stellate hairs, veins scabrous, prominent; petioles slender, 5–7 cm. long, covered very lightly with short suppressed yellowish stellate pubescence. Inflorescence hermaphrodite, terminal, rarely axillary, slightly leafy, about 14 cm. long and 12 cm. wide, rarely larger, the cymes of about 12 flowers rather loose, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels 3–4 mm. long, the buds obovoid, constricted towards the base, with conspicuous appendages at the tips of the sepals, the sepals 5, spatulate, 5–6 mm. long, 3-nerved, with large, about 2 mm. long, reflexed, trigonal appendages at the tips, light green with short suppressed tufts of stellate hairs without, glabrate, yellow to yellowish brown within, the petals 5, linear, slightly shorter than the sepals, about 4 mm. long, 1- to 3-nerved, yellowish brown, the stamens about 40, with filaments about 4–5 mm. long, the ovary orbicular, 1–2 mm. long, sessile, with a slender style about 4 times the length of the ovary, briefly bifid at the tip, and with small acute stigma lobes. Fruit orbicular, sessile, densely stellate-pubescent, 5 mm. in diameter, with a distinct groove in the middle of the fruit body, the fringe dense, of 2–3 rows of plumose bristles shorter than the diameter of the fruit body, about 3 mm. long; the seed plump, ovoid, very slightly grooved, about 2 mm. long.

Distribution: On shady canyon slopes or oak flats in northwestern Mexico, altitude about 500 m. Flowers in September–October and fruits in late October–December.

MEXICO: CHIHUAHUA: Hacienda San Miguel, near Batopilas, E. Palmer 97, 100, 191; Guasaremos, Río Mayo, Gentry 2440, 2909; La Mesa, Gentry 6607; Almaden, Le Sueur 1404. SINALOA: Cerro Colorado, alt. 2000 ft., Gentry 5069; vicinity of Culican, Brandegee s. n. (type of *H. glaber*). SONORA: Canyon Sapopa, Río Mayo, Gentry 1644, 1709.

A very distinct species with nearly glabrous leaves and sessile fruits characteristically grooved in the middle and with flowers bearing relatively large trigonal apical appendages on the sepals.

The leaves in the type of *H. Palmeri* (E. Palmer 191) are slightly more pubescent than those of *H. polyandrus* (E. Palmer 100), but in both they are nearly glabrous and the variation is only one of slight degree. S. Watson mentioned that in *H. Palmeri* the number of stamens is about 20, but I have not been able to find any specimen that answers to the description of *H. Palmeri* with 20 stamens, either in the specimens cited by S. Watson or in others.

4. *HELIOCARPUS ATTENUATUS* S. Wats. in Proc. Amer. Acad. 21:420. 1886. (T.: *E. Palmer* 99).

H. viridis E. E. Wats. in Bull. Torr. Bot. Club 50:120. 1923. (T.: *Rose, Standley & Russell* 12828).

Small shrubs about 2-3 m. high; older branches dark brown, rather slender, slightly pubescent, smooth, irregularly punctate with few white lenticels; younger branches and inflorescence axes softly tomentose with relatively long, light yellowish brown, stellate hairs, smooth. Leaves ovate to very obscurely 3-lobed, 5-costate at

the base and gradually tapering to the caudate-acuminate tip, base cordate or subcordate, irregularly and bluntly serrated, upper surface slightly pubescent, coarse, with many suppressed stellate hairs, scabrous on the veins, lower surface densely stellate-pubescent especially on the veins. Inflorescence hermaphrodite, usually axillary, small, leafy, about 8 cm. long and 10 cm. wide, rarely larger, the cymes of about 16-18 flowers borne loosely in nodose clusters, the flowering peduncles mostly 3-radiate, rarely 2-radiate, about 5-6 cm. long, usually subtended by two short bracteoles, the pedicels 2-3 mm. long, the buds obovoid, very slightly constricted towards the base, with short

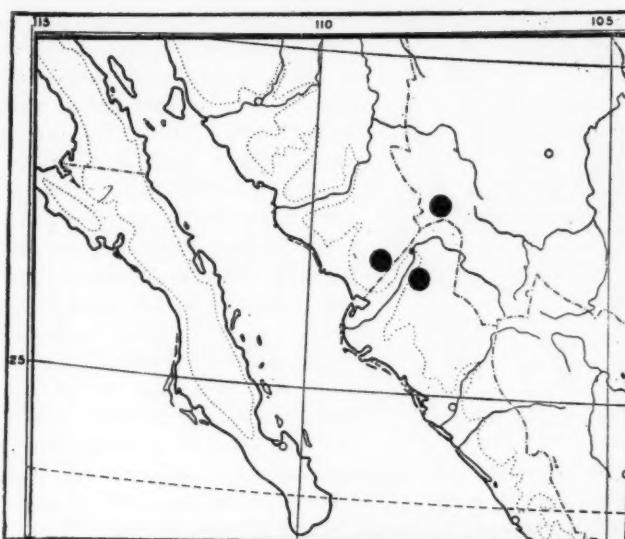


Fig. 4. *H. attenuatus*

appendages on the tips of the sepals, the sepals 3 or 4, linear, 4-5 mm. long, 1- to 3-nerved, the short, erect appendages on the tips 1 mm. long, light green with fine tomentum without, glabrate, yellowish brown within, the petals 3 or 4, linear, shorter than the sepals, 2-3 mm. long, the stamens about 16-20, with the filaments as long as the petals, the ovary ovoid, 1.0-1.5 mm. long, sessile, with a style about twice the length of the ovary, bifid about one quarter of its length and with the stigma lobes acute, spreading. Fruit ovoid, sessile, densely tomentose, 3 mm. long and 2 mm. wide, the fringe of two rows of slender plumose bristles, 6-7 mm. long; the seed ovoid, 1-2 mm. long.

Distribution: Confined entirely to northwestern Mexico, apparently rare, usually growing at altitudes of about 300-500 m. Flowers from August to September and fruits from October to December.

MEXICO: CHIHUAHUA: southwestern Chihuahua, *E. Palmer* 99; Río Benito, *Le Sueur* 661, 1158. SINALOA: Choix, Tasfera, alt. 420 m., *Gonzalez* 860. SONORA: Alamos, *E. Palmer* 647, 733; Sierra de Alamos, *Rose, Standley & Russell* 12828.

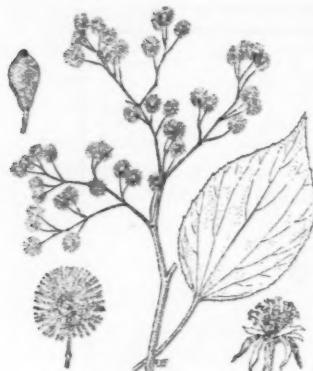
Map 4. Distribution of *H. attenuatus*

This is a very distinct species, with the caudate-acuminate leaves the smallest known for the genus. It does not resemble any other species in its vegetative characters. The leaves of the type of *H. viridis* (Rose, Standley & Russell 12828) are small but not caudate-acuminate. The type is from a relatively young plant and rather poorly preserved. I have not been able to find any other specimen which matches the type, and I am doubtful about the type itself. Except for its small wrinkled leaves, there is nothing which would prevent its identification with *H. attenuatus* (type: E. Palmer 99).

5. *HELIOCARPUS OCCIDENTALIS* Rose, in Contr. U. S. Nat. Herb. 5:127. 1897. (T.: Palmer 440).

H. laevis Rose, loc. cit. 8:317. 1905. (T.: Rose 2860).

Small trees or shrubs about 5–6 m. high; older branches generally glabrate, cream to brownish, slightly rugose, irregularly punctate with white lenticels; younger branches and inflorescence axes covered with rather dense tomentum of short yellowish stellate hairs. Leaves broadly ovate, sometimes rather obscurely 3-lobed, 10–13 cm. long and 8–11 cm. wide, 5- to 7-costate at the base, narrowly acuminate, base rounded or cuneate, rarely subcordate, somewhat regularly and doubly serrated, upper surface generally dark green, glabrate, coarse, with suppressed stellate hairs, veins and veinlets more pubescent with short tufts of yellowish stellate hairs, lower surface slightly more pubescent than the upper, becoming

Fig. 5. *H. occidentalis*

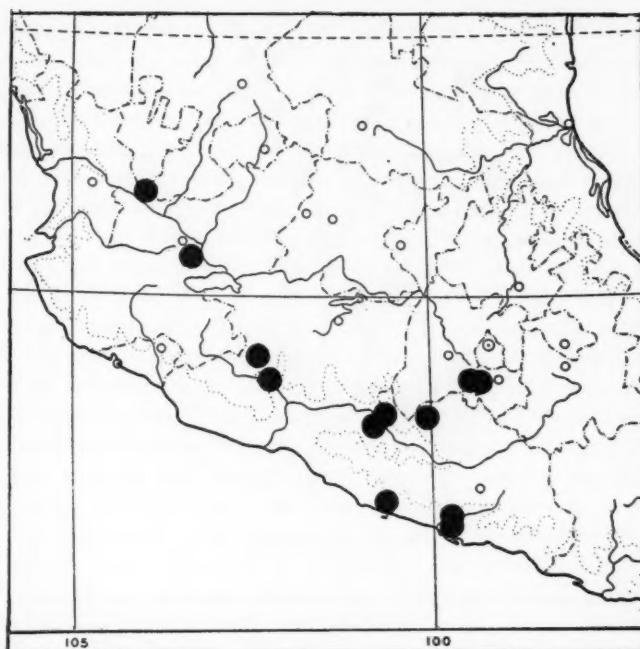
about 1 mm. long, erect, linear appendages at the tips, light green with short stellate hairs without, glabrate, cream or light brown within, the petals 5, rarely 4, linear, nearly as long as the sepals, 1- to 3-nerved, the stamens about 40, with the filaments about 4-5 mm. long, the ovary ovoid, 1.0-1.5 mm. long, sessile, with a short style about twice the length of the ovary, briefly bifid at the tips and with small acute stigma lobes. Fruit orbicular, sessile, punctate with short separate tufts of stellate hairs, about 3 mm. in diameter, the fringe of relatively stout plumose bristles about 8-9 mm. long; the seed ovoid, about 2 mm. long.

Distribution: Plants of central Mexico, growing on hill slopes and chaparrals, between 500 and 1000 m. Flowering in September and October and fruiting from October to December.

MEXICO: CHIAPAS: Manzanillo, *E. Palmer* 986. GUERRERO: Acapulco, *E. Palmer* 440; La Providencia, Acapulco, *Hancock* 12; Iguala Canyon, alt. 2500 ft., *Pringle* 10069; Arecelia-Fragua, Coyuca, *Hinton* 6605; Coyuca, *Hinton* 6901, 6906; Pungarabato, Coyuca, *Hinton* 6876; Atoyac, Galeana, *Hinton* 10901. JALISCO: Bolanos, *Rose* 2860a, 2860b; Guadalajara, *Rose* & *Painter* 7389. MEXICO: Limones, Temascaltepec, alt. 910 m., *Hinton* 6724; Paso del Rio, *Emrick* 192. MICHOACAN: Apatzingan, alt. 2000 ft., *Leavenworth* & *Hoogstraal* 1731; between Acahuato and Apatzingan, *Leavenworth* & *Hoogstraal* 1525; El Ocote, *Langlassé* 623.

The fruits of this species are very characteristic, being nearly orbicular, with short separate tufts of stellate hairs. The small erect sepal appendages and the glabrate leaves make this species an easy one to identify. *H. laevis* (type: *Rose* 2860) which has been identified with many other species actually is conspecific with this.

nearly glabrate when mature, yellowish green, the veins and veinlets covered with dense tufts of yellow stellate hairs; petiole about 6 cm. long, slender, covered lightly with yellow stellate hairs. Inflorescences hermaphrodite, usually axillary, rarely terminal, rather leafy, about 14 cm. long and 10 cm. wide, sometimes much smaller, the cymes of about 12 flowers, rather loose in nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, subtended by two small bracteoles, the pedicels 2-3 mm. long, the buds obovoid, slightly constricted towards the base, with conspicuous appendages at the tips of the sepals, the sepals 5, rarely 4, linear-spatulate, 4-5 mm. long, 3- to 5-nerved, with small,

Map 5. Distribution of *H. occidentalis*

6. *HELOCARPUS MEXICANUS* (Turcz.) Sprague, in Kew Bull. 272. 1921. (T.: *Galeotti 4154*).

Adenodiscus mexicanus Turcz. in Bull. Soc. Nat. Mosc. 19²:504. 1846.

Triumfetta mexicana Turcz. in loc. cit. 31¹:230. 1858.

H. glanduliferus Robinson, in Contr. U. S. Nat. Herb. 5:127. 1897. (T.: Heyde 281).

H. glabrescens Hochr. in Ann. Conserv. et Jard. Bot. Genève 18:122. 1914. (T.: *Galeotti 4154*).

H. costaricensis Sprague, in Kew Bull. 349. 1923. (T.: Pittier 13022).

H. belizensis Lundell, in Phytologia 2:2. 1941. (T.: Gentle 2273).

H. yucatenensis Millsp. in herb.

Small trees or shrubs 5–6 m. high; older branches dark brown, glabrate, slightly rugose, punctate irregularly with minute white lenticels; younger branches and inflorescence axes very lightly scurfy-pubescent, with small clusters of simple and stellate hairs, nearly glabrate. Leaves broadly ovate to ovate-lanceolate, the more mature ones broadly ovate, the younger ones around the inflorescence usually ovate-lanceolate, 5-costate at the base, not lobed, 12–14 cm. long and 6–10 cm. wide, acute to acuminate, base rounded or slightly obtuse, irregularly and bluntly serrated, the basal serrations glandular, upper surface dark green, glabrate with few suppressed stellate hairs, lower surface more pubescent with fine, weak, crisped, stellate

Fig. 6. *H. mexicanus*Map 6. Distribution of *H. mexicanus*

hairs, becoming nearly glabrate at maturity. Inflorescences gynodioecious, axillary, large and very leafy; the hermaphrodite large and spreading, very leafy, about 20 cm. long and 15 cm. wide, the cymes of about 20 flowers, rather loose, the flowering peduncle mostly 3-radiate, about 2-3 mm. long, usually subtended by a pair of small blunt bracteoles, the pedicel about 6-8 mm. long, the buds obovoid, slightly constricted in the middle towards the base, rusty brown, with small appendages at the tips of the sepals, the sepals usually 5, rarely 4, spatulate, about 5-6 mm. long, 1-2 mm. wide, rusty brown and glabrate without, lighter brown and glabrate within, with linear, about 1.5 mm. long, erect appendages on the tips, the petals 5, rarely 4, linear, 1-nerved, 3-4 mm. long, the stamens 24-30, with the filaments as long as the petals, the ovary ellipsoid, 1-2 mm. long, borne on a very short gynophore, with a style about 3 times the length of the ovary, briefly bifid, and with acute, slightly spreading stigma lobes; the pistillate nearly as large as the hermaphrodite, the cymes of about 20 flowers, greatly condensed and crowded in nodose clusters, the flowering peduncles 3-radiate, short, less than 1 mm. long, the pedicels about 1 mm. long, the buds about 2-3 mm. long, appendaged at the tips of the sepals, the sepals 5, linear, about 3 mm. long, appendaged at the tips, rusty brown and glabrate without and within, the petals none, the staminodes about 20-30, the ovary ovoid, less than 1 mm. long, borne on a very short gynophore, with a short style, briefly bifid and with acute stigma lobes. The fruit ellipsoid, glabrate, surface red-glandular, about 6-8 mm. long and 3 mm. wide, with few ridges, borne on a bristly gynophore 2-8 mm. long, the fringe usually of one row of plumose bristles 6-8 mm. long; the seed pyriform, blunt-pointed, about 3-4 mm. long.

Distribution: Plants of southeastern Mexico and northern Central America, growing along roadways, river banks, or on hill slopes; in thickets of bushy slopes or on hill tops in open places. Flowers from September to October and sometimes as late as December, and fruits from November to February.

MEXICO: CAMPECHE: Tuxpuna, Lundell 950, 1192. OAXACA: locality not mentioned, Ghiesbreght 51. VERA CRUZ: Zazuapan, Linden 898; Cordillera, Galeotti 4154; Zazuapan and vicinity, Purpus 2227; Mirador, Liebmann 523; Mirador, Linden 858; rocky barranca near Gaucho, Viejo, Purpus 15704a. YUCATAN: Pocoboch, Chac tolol, Gaumer 1315; San Anselmo, Gaumer 1234; Calotmul, Gaumer 2302; Chichankanab, Gaumer 2275; Xnoca, Gaumer 23488, 24177.

BRITISH HONDURAS: El Cayo District, Vaca, Gentle 2273; Jacinto Hills, alt. 600 ft., Schipp S-589.

GUATEMALA: ALTA VERAPAZ: southwest of Lanquin, alt. 600-1000 m., Steyermark 44076. CHIMALTENANGO: along Rio Guacalate, southwest of Chimaltenango, alt. about 1700 m., Standley 80064, 81067; Chimaltenango, Johnston 1106, 1332. CHIQUIMULA: Volcán Ipala, near Amatillo, alt. 900-1510 m., Steyermark 30377. GUATEMALA: exact locality lacking, Aguilar 81; alt. 1485 m., Morales 1.122. JUTIAPA: Volcán Suchitan, northwest of Asuncion Mita, alt. 600-2050 m., Steyermark 31912. SACATEPEQUEZ: near Pastores, alt. 1560-1650 m., Standley 59888; near Antigua, alt. 1500-1600 m., Standley 64273. SANTA ROSA: above Cerro Redondo, Steyermark 52218; near Cuilapilla, alt. about 900 m., Standley 78068; Chupadero, alt. 5000 pp., Heyde & Lux 3956. DATA INCOMPLETE: Heyde 381.

HONDURAS: EL PARAISO: Guinope, alt. 1430 m., Rodriguez 1679.

EL SALVADOR: vicinity of San Salvador, *Renson 61*; vicinity of San Salvador, alt. 650-850 m., *Standley 19660*.

COSTA RICA: SAN JOSÉ: *Río Torres*, alt. 1100 m., *Tonduz 7451*; *bords de Río Torres près San Francisco de Guadalupe*, alt. 1100 m., *Tonduz 8453*.

This species has been described by most authors as having sessile fruits. Actually the fruits are borne on a gynophore the length of which varies from 2 to 8 mm. Many species have been named because of the extreme variability of the length of the gynophore. The correlation of the flowering with the fruiting specimens has been greatly confused.

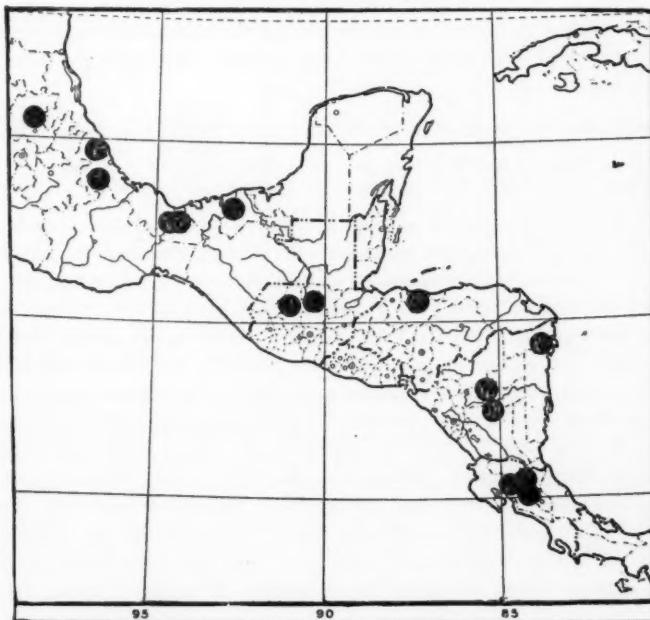
H. mexicanus (type: *Galeotti 4154*) can be recognized easily by its brown glabrate fruits borne either on a very short or on a slightly longer gynophore. In flower, this is one of the easiest species to identify because of the large erect appendages on the tips of the sepals and the nearly glabrate ovate-lanceolate leaves, as well as by the leafy axillary inflorescence.

This species actually is a link between the sessile-fruited and the stipitate groups. It has the characteristics of both the groups.

7. *HELIOCARPUS APPENDICULATUS* Turcz. in Bull. Soc. Nat. Moscou 31¹:226. 1858. (T.: *Linden 2065*).

H. chontalensis Sprague, in Kew Bull. 350. 1923. (T.: *Lévy 483*).

Trees 12-14 m. high; older branches dark brown, scurfy, ferruginous-tomentose with both simple and stellate hairs, rarely glabrate, ridged, punctate irregularly with small, white lenticels; younger branches and inflorescence axes covered with thick, scurfy, ferruginous tomentum. Leaves broadly ovate, sometimes obscurely 3-lobed, 14-16 cm. long and 12-14 cm. wide, 5- to 7-costate at the base, acuminate, base subcordate or rounded, with two conspicuous leafy auricles at the basal sinus, each about 5-7 mm. wide and 4-5 mm. long, unequally and bluntly serrated, the basal serrations glandular, upper surface dark green, glabrate, with few suppressed, compact tufts of stellate hairs, lower surface whitish, with dense stellate tomentum, petioles relatively stout, about 6-8 cm. long, covered with dense scurfy, ferruginous tomentum. Inflorescences hermaphrodite, usually terminal, rarely axillary, slightly leafy, about 15 cm. long and 12-14 cm. wide, the cymes of about 16-18 flowers, rather loose, the flowering peduncles 3-radiate, about 2-3 mm. long, the pedicels 3-4 mm. long, the buds obovoid, slightly constricted in the middle, rather large for the genus, about 6 mm. long, not appendaged at the tips of the sepals, the sepals 4, linear, 6-7 mm. long, light green with short separate tufts of stellate hairs without, glabrate, yellow-brown within, the petals 4, spatulate, 3-nerved, 3-4 mm. long, the stamens about 30, with filaments about 4-5 mm. long, the ovary ellipsoid, 1-2 mm. long, borne upon a gynophore about the length of the ovary itself, with a style about twice the length of the ovary, bifid about half its length and with small, acute, spreading stigma lobes. The fruit suborbicular, about 5 mm. long and 3-4 mm. wide, densely tomentose, borne upon a gynophore about 5-8 mm. long, with 2-3 pairs of plumose bristles, the fringe of 1 or 2 rows of plumose bristles about 6-8 mm. long; the seed pyriform with a shallow groove, slightly stellate-pubescent, about 2-3 mm. long.

Fig. 7. *H. appendiculatus*Map 7. Distribution of *H. appendiculatus*

Distribution: Plants of central Mexico and Central America: a species of relatively wide distribution, usually growing along river banks or roadways in secondary growth subjected to seasonal floods; at times forming a pure stand in moist places, usually in heavy red clay loam, at various altitudes but most abundant above 1000 m. Flowers from December to about the middle of March and fruits persistent up to about the middle of June.

MEXICO: SAN LUIS POTOSI: near Tancanhuitz, *Nelson* 4383. TABASCO: locality lacking, alt. 300 m., *Linden* 1609; Teapas, *Linden* 2065. VERA CRUZ: Fortuno, Coatzacoalcos River, alt. 30-50 m., *L. Williams* 8273, 8288, 8289, 8400, 8526, 8527; Rio Seco prope Cordoba, *Woronow* 2963; Mirador, *Linden* 469; near Jalapa, *Rose & Hough* 4314.

GUATEMALA: ALTA VERAPAZ: Pansamala, alt. 3800 pp., *J. D. Smith* 1723; 2½ miles west of Cubilquitz, alt. 250-300 m., *Steyermark* 44342; trail from Senahu to Actala, *Maxon & Hay* 3305, 3306, 3322; Cubilquitz, alt. 350 m., *Tuerckheim* 7828. HUEHUE-TENANGO: between Maxbal and Xoxlac, Sierra de los Cuchumatanes, alt. 1500-1600 m., *Steyermark* 48987; Cerro Chiblac, between Finca San Rafael and Ixcán, Sierra de los Cuchumatanes, alt. 1200-2000 m., *Steyermark* 49169.

HONDURAS: ATLANTIDA: Lancestilla Valley, near Tela, alt. 20-600 m., *Standley* 54096. NICARAGUA: SEGOVIA: region of Braggman's Bluff, *Englesing* 136, 140; Chontales, alt. 600 m., *Lévy* 483; Chontales, *Tate* 31 (384).

COSTA RICA: CARTAGO: Rubber Plant Investigation Station, Turrialba, *Aguilar* 97100. GUANACASTE: upper slopes of Cerro San José de Libano, alt. 500-900 m., *Dodge*, *Hancock* & *Thomas* 6379. SAN JOSÉ: vicinity of El General, alt. 700 m., *Skutch* 3922; vicinity of El General, alt. 670 m., *Skutch* 4226. DATA INCOMPLETE: *Rowlee & Rowlee* 212; Tibarcia, alt. 980 m., *Solis R.* 534; Santiago, *Brenez* 655.

An extremely easy species to identify due to the presence of two conspicuous auricles at the basal sinus of the relatively large leaf. The fruits are suborbicular and tomentose.

8. *HELIOCARPUS AMERICANUS* L. Sp. Pl. ed. 1, 448. 1753. (T. in Br. Mus.).^{8, 9}

H. tomentosus Turcz. in Bull. Soc. Nat. Moscou 31:255. 1858. (T.: *Linden* 857).
H. americanus var. *typica* K. Schum. in Martius, Fl. Bras. 12³:141. 1886.

Small trees 3-5 m. high; older branches light brown, glabrate, smooth, irregularly punctate with many small white lenticels; younger branches and inflorescence axes lightly tomentose with both stellate and simple hairs. Leaves ovate, not lobed, 10-12 cm. long and 6-8 cm. wide, 5-costate at the base, acuminate, base rounded or obtuse, never cordate, irregularly and bluntly serrated, upper surface dark green, glabrate with few highly suppressed stellate hairs, lower surface whitish, very densely tomentose with both long stellate and simple hairs; petioles relatively stout, about 4 cm. long, very densely tomentose. Inflorescences hermaphrodite, terminal, about 15 cm. long and 12 cm. wide, sometimes very slightly leafy, the cymes of about 18-20 flowers, densely crowded in nodose clusters, the flowering peduncles 3-radiate, short, about 1 mm. long, the pedicels about 1-2 mm. long, the buds obovoid, slightly constricted towards the base, without appendages at the tips of the sepals, the sepals 4, spatulate, 4-5 mm. long, light green and densely tomentose without, glabrate, yellow to yellow-brown within, the petals 4, linear, 1-nerved,

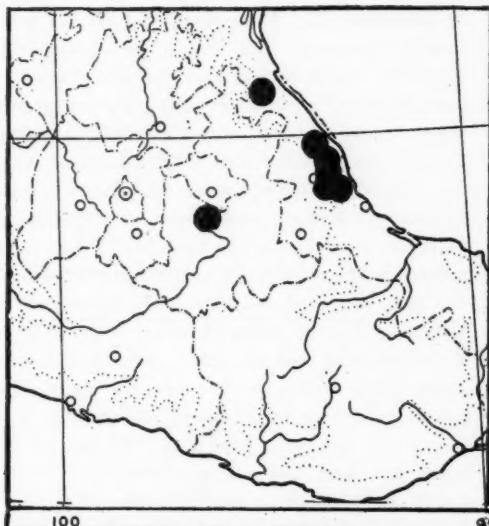
⁸Jour. Bot. 36:131. 1898.

⁹Bot. Gaz. 61:256. 1923.

about 2-3 mm. long, the edges slightly ciliate, the stamens about 20, with the filaments about 3 mm. long, the ovary ovoid, about 1 mm. long, borne on a short gynophore, with a style about 2-3 times the length of the ovary, bifid about one quarter of its length and with acute, spreading stigma lobes. Fruit ovoid, densely tomentose, becoming slightly less so with age, about 3-4 mm. long and 2-3 mm. wide, borne on a long bristly gynophore about 5-8 mm. long, with 2-3 pairs of plumose bristles, the fringe of two rows of plumose bristles about 4-6 mm. long; the seed ovoid, about 1.5 mm. long and 1.0 mm. wide, with a distinct groove in the middle, slightly stellate-pubescent.



Fig. 8. *H. americanus*



Map 8. Distribution of *H. americanus*

Distribution: Plants of central and southeastern Mexico, growing at altitudes between 400-1200 m. Flowers in January and February and the fruits are persistent up to the middle of May.

MEXICO: OAXACA: locality not mentioned, Galeotti 4162, 4162b. PUEBLA: Huachinango, convallis torrentis, alt. 1100 m., Fröderström & Hulten 860. VERA CRUZ: Zazuapan and vicinity, Purpus 2220, 2387; Zazuapan, Purpus 8275; Mirador, Liebmann 475; Orizaba, Botteri 340, 341, 882, 888, 922; Vallee de Cordova, Bourgeau 1819, 1974; Mirador, alt. 400 m., Linden 857; Cordova, J. G. Smith 284; near Jalapa, Rose & Hough 4304; Estacion El Fortin, Orizaba, Conzatti 1694; near Orizaba, alt. 4000 ft., Pringle 6106; Sanborn, Orcutt 3068; circa Cordoba, Woronow 2947; Rio Seco prope Cordoba, Woronow 3038; Cordoba, Greenman 161; barranca of Chevastl near Huatusco, Rozynski 782. DATA INCOMPLETE: Sumichrast 882.

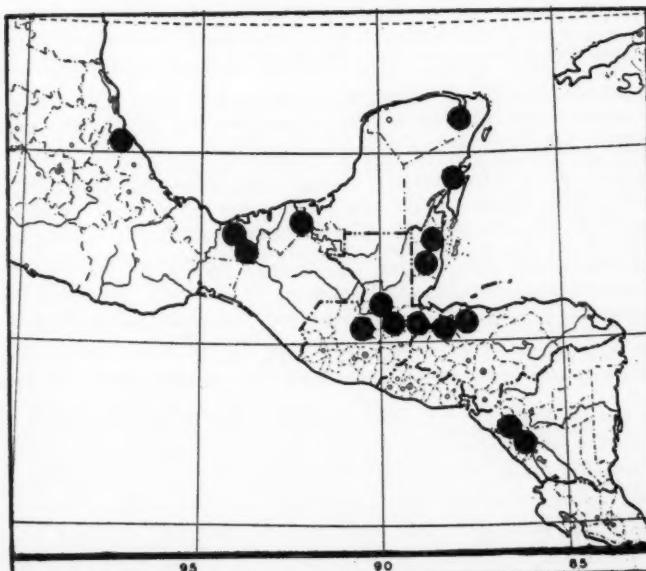
The identity of *H. americanus* is based on the interpretations by E. G. Baker⁸ and T. A. Sprague.⁹

This species has very characteristic ovate-lanceolate leaves, which are densely tomentose only on the lower surface.

9. *HELIOCARPUS DONNELL-SMITHII* Rose, in Bot. Gaz. 31:110. 1901. (T.: J. D. Smith 1722).*H. Caeciliae* Loesener, in Fedde, Rep. Spec. Nov. 12:227. 1913. (T.: Seler 4976).*H. horridus* Lundell, in Bull. Torr. Bot. Club 66:597. 1939. (T.: Lundell & Lundell 7821).*H. cuspidatus* Lundell, in Phytologia 2:2. 1941. (T.: Gentle 2297).*H. floribundus* Lundell, loc. cit. 1941. (T.: Gentle 1534).

Small trees about 10 m. high; older branches glabrous, smooth, yellow to yellowish brown, irregularly punctate with white lenticels; younger branches and inflorescence axes slightly pubescent with short stellate and simple hairs. Leaves broadly ovate, 12–14 cm. long and 8–10 cm. wide, not lobed, 5-costate at the base, shortly acuminate, base rounded or obtuse, irregularly serrated, lower serrations glandular, upper surface dark green, essentially glabrous with short greatly suppressed stellate hairs, lower surface lighter green, slightly more pubescent than the upper, nearly glabrate, with short stellate pubescence; petioles glabrous, smooth, 6–8 cm. long. Inflorescences gynodioecious, usually terminal, rarely axillary; the hermaphrodite large and spreading, about 18 cm. long and 15 cm. wide, the cymes of about 20 flowers, rather loose, the flowering peduncle mostly 3-radiate, rarely 2-radiate, 2 mm. long, the pedicels 4–5 mm. long, the buds obovoid, slightly constricted in the middle, not appendaged at the tips of the sepals, the sepals 4, linear, 4–6 mm. long and 1–2 mm. wide, light green with stellate pubescence without, glabrate, yellow to yellowish brown within, the petals 4, linear-spatulate, 3-nerved, slightly shorter than the sepals, about 4 mm. long, the stamens 12–16, with filaments about as long as the petals, the ovary ellipsoid, about 1–2 mm. long, borne upon a gynophore nearly as long or very slightly shorter than the ovary itself, with a style 3–4 mm. long, bifid about one quarter of its length and with stigma lobes acute, spreading; the pistillate greatly condensed and crowded, about 5 cm. long and 5 cm. wide, the cymes of about 20 flowers, crowded in nodose clusters, the flowering peduncles very short, 3-radiate, bearing 2 small bracteoles, the pedicels 1–2 mm. long, the buds about 2–3 mm. long, not appendaged at the tips of the sepals, the sepals 4, linear, 2–3 mm. long, light green and slightly pubescent without, generally brownish and glabrate within, the petals none, the staminodes none, the ovary suborbicular, about 1 mm. long, borne upon a very short gynophore shorter than the length of the ovary, with a style nearly twice the length of the ovary, very briefly bifid, the stigma lobes acute. The fruit ellipsoid, nearly glabrate at maturity, slightly rugose, 5 mm. long and 3 mm. wide, borne on a gynophore 8–12 mm. long, bearing 2–4 pairs of plumose bristles, the fringe of two rows of plumose bristles 5–7 mm. long; the seed obliquely ovoid, 2–3 mm. long and about 2 mm. wide, with a distinct groove in the middle.

Distribution: Plants of southern Mexico and Central America. This species is of rather wide continental distribution but its presence in Martinique is difficult to explain, unless through introduction. It is abundant on the edges of forest, in secondary growth, and on mountain slopes at altitudes from 100 to 1500 m. Flowers from December to February, and the fruits are persistent up to June.

Fig. 9. *H. Donnell-Smithii*Map 9. Distribution of *H. Donnell-Smithii*

MEXICO: OAXACA: Tuxtepec, Chiltepec and vicinity, Calderón 452. QUINTANA ROO: Coba, Lundell & Lundell 7821. TABASCO: Atasta, Rovirosa 120. VERA CRUZ: Montzorongo, J. G. Smith 234; Wartenberg, near Tantoyuca, prov. Huasteca, Ervendberg 225; Santa Luceria, Mell 670; Coatzacoalco, isthmus of Tehuantepec, C. L. Smith 1002; district San Andres Tuxtla, Salto de Chilapan, Seler 4976.

BRITISH HONDURAS: Belize District, Gracie Rock, Sibun River, Gentle 1534; El Cayo District, Vaca, Gentle 2297; El Cayo District near Camp 6, Gentle 2355; Inacahual, Stann Creek District, Middlesex, Gentle 2788; Middlesex, Stevenson 3336; 22 Mile, alt. 200 ft., Schipp 872.

GUATEMALA: ALTA VERAPAZ: Arenal, alt. 3000 pp., J. D. Smith 1722; Savanna, north of Concepcion, 3-5 miles southeast of Finca Yalpemech, near Alta Verapaz-Peten boundary line, alt. 100-110 m., Steyermark 45229; southwest of Lanquin, alt. 600-1000 m., Steyermark 44007, 44008; Semacoch, trail to Panzas, Goll 255; road to Sepaciute, Wilson 1978; mountain slopes above Finca, Semay, Wilson 198. IZABAL: between Los Amates and Izabal, Kellerman 6448. SUCHITEPEQUEZ: Mazatenango, alt. 300 m., Kellerman 6068.

HONDURAS: ATLANTIDA: vicinity of Tela, alt. 20-600 m., Standley 55518.

NICARAGUA: MANAGUA: vicinity of Managua, Garnier 560. GRANADA: Volcán Mombacho, Baker 2490.

MARTINIQUE: bois près Fort de France, Hahn 1340; St. Pierre, Curran 7.

This species is characterized by its ellipsoid, nearly glabrate fruits borne on a long bristly gynophore, and by its ovate leaves, which are nearly blabrous to glabrate.

10. *HELIOCARPUS POPAYANENSIS* HBK. Nov. Gen. Sp. 5:341. 1821. (T.: *Humboldt* & *Bonpland*, in *Herb. Paris*).

H. trichopodus Turcz. in Bull. Soc. Nat. Moscou 31¹:226. 1858. (T.: *Funck* & *Schlim* 150).

H. americanus var. *popayanensis* (HBK.) K. Schum., in Martius, Fl. Bras. 12³:141. 1886.

H. popayanensis var. *Schumannii* E. G. Baker, in Jour. Bot. 36:132. 1898.

H. popayanensis var. *Purdiea* E. G. Baker, loc. cit. 1898.

H. popayanensis var. *trichopoda* (Turcz.) E. G. Baker, loc. cit. 1898.

H. popayanensis var. *grandifolius* Hochr. in Ann. Conserv. et Jard. Bot. Genève 18:116. 1914. (T.: Bang 1455).

H. diclinus Hochr. loc. cit. 117. 1914. (T.: H. H. Smith 1908).

H. boliviensis Hochr. loc. cit. 118. 1914. (T.: Bang 1491).

H. stipulatus Hochr. loc. cit. 121. 1914. (T.: Poeppig 3102).

H. Rosei Hochr. loc. cit. 119. 1914. (T.: Bang 2305).

H. americanus acc. to E. E. Wats. in Bull. Torr. Bot. Club 50:123. 1923, not L.

H. australis E. E. Wats. loc. cit. 124. 1923. (T.: Hassler 557).

H. rufus E. E. Wats. loc. cit. 126. 1923. (T.: Pittier 3082).

H. subtrilobus Sprague, in Bot. Gaz. 61:257. 1923. (T.: Fendler 1277B).

Trees usually about 8-10 m. high or more; older branches glabrate, slightly rugose, cream to brown, irregularly punctate with few, rather small, white lenticels; younger branches and sometimes a few of the older branches covered lightly with ferruginous tomentum of both stellate and long coarse simple hairs. Leaves usually 3-lobed with acuminate apices, but sometimes only obscurely so, about 16-20 cm. long and 14-18 cm. wide, base markedly cordate on mature leaves, younger leaves usually with rounded bases, irregularly serrated, upper surface generally dark green, glabrate with short ferruginous stellate tomentum, especially on the veins and veinlets, lower surface light green, slightly more pubescent than the upper, the

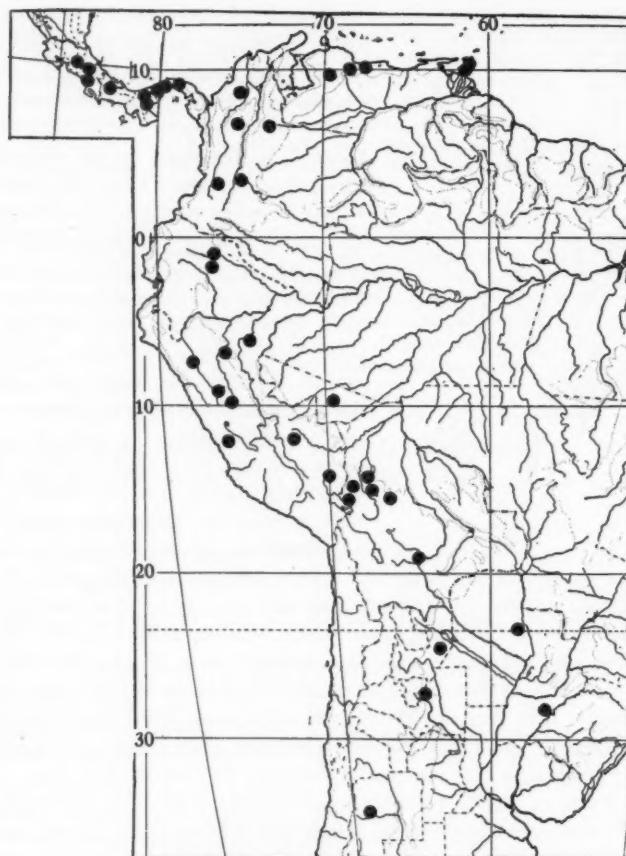


Fig. 10. *H. popayanensis*

pubescence varying from densely stellate to thinly suppressed stellate, the principal veins usually with simple hairs about 2 mm. long; petioles 6–8 cm. long, usually densely covered with both stellate and simple hairs. Inflorescences gynodioecious, usually terminal; the hermaphrodite about 12 cm. long and 14 cm. wide, the cymes of about 12–16 flowers, the flowering peduncles 3-radiate, about 1–2 mm. long, the pedicels about 2–3 mm. long, the buds obovoid, slightly constricted towards the base, without appendages at the tips of the sepals, the sepals 4, spatulate, generally 3-nerved, about 5 mm. long, light green and densely tomentose without, glabrate and yellowish brown within, the petals 4, spatulate, about 3–4 mm. long, slightly ciliate, the stamens about 12–16, with the filaments about 3–4 mm. long, the ovary suborbicular, laterally compressed, about 1.0–1.25 mm. long, borne on

a gynophore about 0.75 mm. long, with a style about twice the length of the ovary, bifid about one quarter of its length and with the stigma lobes spreading, each with 3 acute lobes; the pistillate rather large, much larger than the hermaphrodite, about 14 cm. long and 20 cm. wide, the cymes of 12–16 flowers, rather condensed in nodose clusters, the flowering peduncles 3-radiate, less than 1 mm. long, the pedicels about 1 mm. long, the buds about 3 mm. long, the sepals 4, linear, about 3 mm. long, light green, stellate-tomentose without, glabrate, cream to light brown within, the petals none, the staminodes about 12, the ovary suborbicular, about 1 mm. long, borne on a short gynophore, with a style about twice the length of the ovary, bifid about one quarter of its length and with spreading stigma lobes, each with 3 acute lobes. The fruit ellipsoid to ovoid, with many short tufts of stellate hairs, slightly pubescent, about 5–6 mm. long and 2–3 mm. wide, borne on a bristly gynophore about 1.0–1.5 mm. long with 2–3 pairs of plumose bristles, the fringe of two rows of plumose bristles about 8–12 mm. long; the seed ovoid, about 2 mm. long, with a shallow depression in the middle.

Distribution: A species which extends from Costa Rica to northern Argentina. It is primarily South American and is the only species known there. In southern Central America and northern South America it is found in highlands above 1000 m. altitude, while in Paraguay and Argentina it is usually at lower elevations. *H. popayanensis* frequents steep slopes in forested river valleys, thickets, or in sunny bushy slopes, usually in second growth in cut-over forests. It is abundant in rain or cloud forests or on the edges of forests at stream sides. Flowers in its northern



Map 10. Distribution of *H. popayanensis*

range from December to January and in its southern range from May to June. Fruits persistent in the north until about the middle of March and in the south to about the end of September.

COSTA RICA: ALAJUELA: hills west of Zapate, San Carlos, alt. 1550 m., A. Smith NY1263; Zacero, upper continental divide, alt. 1800 m., A. Smith HI358. HEREDIA: Vera Blanca de Sapiqui, near slope of Central Cordillera, between Poas and Barba volcanoes, alt. 1680 m., Skutch 3346. SAN JOSÉ: La Palma de San Ramon, Brenez 6369; Carpintera, alt. 5700 ft., Stork 1158. DATA INCOMPLETE: Charco, Goicochea, alt. 1400 m., Jimenez 993.

PANAMA: CANAL ZONE: Cerro Gordo, near Culebra, alt. 50-290 m., Pittier 2305; Barro Colorado Island, Frost 218; Canal Zone and vicinity, C.16, back of Curundu, Harvey 5258; Barro Colorado Island, Shattuck 662, 754; near lab., Barro Colorado Island,

1949]

KO KO LAY—REVISION OF HELIOCARPUS

535

Woodworth & Vestal 730, 748; Barro Colorado Island, Wetmore & Abbe 108; Empire Station, Hayes 437. CHIRIQUI: valley of the upper Rio Chiriquí Viejo, White 20; around Camp Aguacatal, eastern slope of Chiriquí Volcano, alt. 2100–2200 m., Pittier 3082; vicinity of "New Switzerland" central valley of Rio Chiriquí Viejo, alt. 1800–2000 m., Allen 1398; vicinity of Cerro Punta, alt. 2000 m., Allen 1519. COCLÉ: hills south of El Valle de Antón, alt. 600–800 m., Allen 2849, 2912; El Valle de Antón, alt. 600–800 m., Hunter & Allen 304. DARIÉN: locality not mentioned, Macbride 2713.

TRINIDAD: St. Ann's Cascade, Broadway 6569; Santa Cruz, Simmonds 281; Lady Chancellor Road, St. Ann's, Broadway 9200; Knagg's Hill, R. O. Williams 12671; St. Cruz, collector unknown 649, 650.

COLOMBIA: ANTIOQUIA: vicinity of Medellin, Toro 206. BOYACÁ: 130 m. n. of Bogota, El Umbo, alt. 3700 ft., Lawrence 590. CAUCA: El Tambo in silva, alt. 1700 m., Sneider 434; highlands of Popayan, alt. 1400–2000 m., Lehmann 5502; Rio Toribio region, alt. 100–1200 m., Espíñola & Giacometti 20861; cerca de Popayan, matorrales en Rio Blanco, alt. 1800 m., Arbelaez & Cuatrecasas 5798. MAGDALENA: Santa Marta, alt. 2000 ft., H. H. Smith 1908; Pita, André 407. NARINO: frontera Colombo-ecuatoriana, selva higrofílica del Rio San Miguel, junto a la desembocadura del Rio Conejo, alt. 300 m., Cuatrecasas 10925. NORTE DE SANTANDER: Cordillera Oriental, region del Sarare, Quebrada de la China (en la Hoya del Cubugon), Santa Librada en El Reposo, alt. 800 m., Cuatrecasas 13262, 13340; Cordillera Oriental, region del Sarare, Hoya del Rio Chitaga entre Chorro Colorado y Bata, alt. 1300 m., Cuatrecasas, Schultes & Smith 12237; Cordillera Oriental, region del Sarare, La Cabuya, alt. 1300 m., Cuatrecasas, Schultes & Smith 12590; Cordillera Oriental, region del Sarare, entre el Alto del Loro y el Alto de Santa Ines, bosques, alt. 1800–2000 m., Cuatrecasas, Schultes & Smith 12471.

VEZELA: DISTRITO FEDERAL: Caracas, alt. 3000 pp., Funck & Schlim 150; Carteza, alt. 930 m., L. Williams 9957. MERIDA: prope coloniam Tovar, Fendler 1277, 1277B. MIRANDA: La Malva, near Las Mostazas, Allart 273; La Malva, cerca de las Mostazas, Pittier 273; in valley from El Valle to Cua, Pittier 11975; en matorrales a lo largo de la carretera de los Teques, alt. 1200 m., L. Williams 10692. YARACUY: Hacienda Iboea near San Pablo, Pittier 12605. DATA INCOMPLETE: Las Trincheras, Warming 313; al sur de Rio Claro, alt. 1360 m., Saer 778.

BRAZIL: ACRE: near mouth of Rio Macauhan (tributary of Rio Yaco), lat. 9.20' S., and long. 69. W., Kruckoff 5261.

ECUADOR: AZUAY: along Rio Patul between Hacienda Yubay and Hacienda San José de Caimotan, in region of Sanaguan, alt. 850 m., Steyermark 52754; Hacienda Yubay, at Sanaguan, on south side of Rio Patul, alt. 850 m., Steyermark 52694; Rio Norcay between Rio Gamolatal and Rio Norcay, alt. 1095–1370 m., Steyermark 52878. CHIMBORAZO: Chimbo, alt. 1000 m., Rimbach 288. DATA INCOMPLETE: vicinity of Ventura, Rose & Rose 23518.

PERU: CAJAMARCA: Guerocotillo, Prov. Contervo, alt. 2000 m., Weberbauer 7124. CUZCO: Rio Chaupimayo, Convencion, Soukup 790. HUANUCO: Monzon, alt. 900–1000 m., Weberbauer 3432; Cueva Grande, estacion near Pozuzo, alt. 3500 ft., Macbride 4765; Vinayacu, Sawada 101. JUNIN: Chanchamayo Valley, alt. 1500 m., Schunke 290, 293; Pichis Trail, Dos de Mayo, alt. 1700–1900 m., Killip & Smith 25864. LORETO: Muna, Macbride 4065; lower Rio Huallaga, alt. 155–210 m., Klug 3076; west of Tarapota, Spruce 4558. SAN MARTIN: Juan Jui, alto Rio Huallaga, alt. 400–800 m., Klug 4395. DATA INCOMPLETE: Poeppig 1894, 3102; Ruiz & Pavon 39/8, 39/9.

BOLIVIA: COCHABAMBA: Incachaca—S. Antonio, alt. 1500 m., Werdemann 2126. LA PAZ: Calapampa, Coroico, Bang 2305; Mapiri, Bang 1491; Guanai-Tipuani, Bang 1455; Guanai, alt. 2000 ft., Rusby 1492; Beni River, Rusby 1493; Moryungas, Region von Coripata, Hacienda "El Choro", Buchtien 8125; Province of S. Yungas, basin of Rio Bopi, San Bartoloma (near Calisaya), alt. 750–900 m., Kruckoff 10249, 10283, 10409. SANTA CRUZ: Legunillas, Cordillera de Tecausasi, alt. 1600 m., Cardenas 2839.

ARGENTINA: CATAMARCA: Del Alto, Bategua, alt. 1250 m., Venturi 7074. MISIONES: vicinity of Puerto Aguirre, alt. 100 m., Curran 9, 17; vicinity of Puerto Leon, alt. 75–100 m., Curran 700, 718. TUCUMAN: Famailla, San Pablo, alt. 600 m., Venturi 1002, 1002C;

Famailla, San Rafael, *Venturi* 9205; locality not mentioned, *Hsuman* 9206.
HAWAII: Oahu, planted in foothills for reforestation, *Degener* 10843.

The plants of this species have leaves whose diversity of shape and size is unparalleled in the whole genus. A general tendency is for the plants in the central range of the species to have leaves more definitely and acutely 3-lobed than those towards either the northern or the southern limits, where the leaves frequently may be quite undivided. The pubescence varies from slightly tomentose to nearly glabrate. The constant characters throughout its wide distribution are the hirsute indumenta on the lower nerves, the sepals without appendages, the 3-parted stigma lobes, and the fruits, which are ellipsoid to ovoid and slightly tomentose.

11. *HELIOCARPUS NODIFLORUS* (Donn. Sm.) Donn. Sm. & Rose, in Contr. U. S. Nat. Herb. 5:126. 1897.

H. polyandrus var. *nodiflorus* Donn. Sm. in Bot. Gaz. 23:240. 1897. (T.: Heyde & Lux 4329).

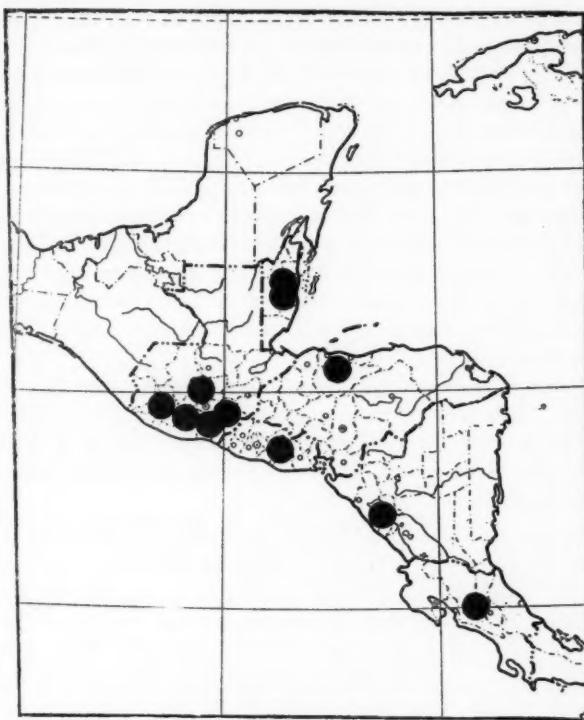
H. excelsior Morton, in Jour. Wash. Acad. Sci. 27:307. 1937. (T.: Skutch 2250).

H. Gentleii Lundell, in Phytologia 2:2. 1941. (T.: Gentle 1787).



Fig. 11. *H. nodiflorus*

Trees about 10–18 m. high; older branches glabrate, longitudinally ridged, light brown, punctate irregularly with few white lenticels; younger branches and inflorescence axes scurfy, slightly ferruginous-pubescent with both simple and stellate hairs. Leaves 3-lobed, sometimes obscurely so, generally medianly oblique, large, 16–18 cm. long and 15–18 cm. wide, 5- to 7-costate at the base, acute to



Map 11. Distribution of *H. nodiflorus*

acute, base usually cordate, sometimes slightly rounded, rather regularly and doubly serrated, lower serrations slightly glandular, upper surface dark green, glabrate, with few tufts of short stellate hairs in the nerve axes, lower surface light green, slightly more pubescent than the upper, especially in the nerve axes; petioles large and stout, about 10 cm. long, lightly ferruginous-stellate-pubescent, scurfy; stipules sometimes persistent. Inflorescences gynodioecious, usually terminal, large and spreading; the hermaphrodite about 15 cm. long and 18 cm. wide, the cymes of about 15–20 flowers borne in compact nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels 1–3 mm. long; the buds obovoid, slightly constricted in the middle towards the base, sometimes with small acute appendages on the tips of the sepals, the sepals 4, spatulate, 4–5 mm. long, light green with stellate tomentum without, glabrate and yellowish brown within, the petals 4, linear, 1-nerved, about 4 mm. long, the stamens about 20–24, with the filaments about 4 mm. long, the ovary ovoid, slightly compressed, about 1.5 mm. long, borne on a short gynophore less than 1 mm. long, with a style about 3–4 mm. long, bifid about half its length at anthesis and with the stigma lobes acute and spreading; the

pistillate about as large as the hermaphrodite, the cymes of about 20 flowers, rather compressed and crowded in nodose clusters, the flowering peduncles 3-radiate, less than 1 mm. long, the pedicels about 1-2 cm. long, the buds about 2-3 mm. long, usually not appendaged at the tips of the sepals, the sepals 4, linear, about 2-3 mm. long, light green and stellate-pubescent without, glabrate and yellowish brown within, the petals none, the staminodes about 12-16 or none, the ovary ovoid, small, about 1 mm. long, slightly compressed, borne on a short gynophore, with a style slightly longer than the ovary, briefly bifid and with the stigma lobes acute. Fruit orbicular, slightly tomentose with short separate tufts of stellate hairs, about 5-6 mm. in diameter, borne on a bristly gynophore 10-15 mm. long, bearing 2-3 pairs of plumose bristles, the fringe of 1 or 2 rows of plumose bristles 6-8 mm. long; the seed obliquely ovoid, about 2-3 mm. long, with a distinct groove in the middle.

Distribution: A species primarily of Central America, extending into southeastern Mexico. It is common in clearings and in wet thickets, nearly always in secondary growth besides rivers or in sheltered valleys, usually at altitudes from 1000 to 2500 m. Flowers from January to February, the fruits persisting until about the middle of April.

BRITISH HONDURAS: Gracie Rock, Sibun River, *Gentle* 1787; Stann Creek Valley, 17 miles, *Gentle* 3202, 3203, 3204; Stann Creek Valley, Big Eddy Creek, *Gentle* 3470; Little Coquericot, Belize River, *Lundell* 4177.

GUATEMALA: CHIMALTENANGO: lower and middle southwestern slopes of Volcán Fuego, above Finca Montevideo, along barranco Espinazo and tributary of Río Pantaleón, alt. 1200-1600 m., *Steyermark* 52113. EL PROGRESO: Montana Canahui, between Finca San Miguel and summit of mountain, near upper limit of Finca Caieta, alt. 1600-2300 m., *Steyermark* 43825. ESCUITLA: between Río Jute and Río Pantaleón, on road between Escuintla and Santa Lucía Cotz, alt. 540-720 m., *Standley* 63443. QUEZALTENANGO: Pueblo Nuevo, alt. 500-600 m., *Steyermark* 35467; Colomba, alt. 3000 ft., *Skutch* 2037. QUICHE: Nebaj, alt. up to 6200 ft., *Skutch* 1763. SAN MARCOS: between Rodeo and Malacate, alt. 1400-3500 ft., *Nelson* 3742. SANTA ROSA: Río Pinula, alt. 4000 pp., *Heyde & Lux* 4329; Naranjo, alt. 1100 m., *Heyde & Lux* 4177.

HONDURAS: ATLANTIDA: Lancestilla Valley, near Tela, alt. 20-600 m., *Standley* 53854, 55791, 55793, 56640.

NICARAGUA: GRANADA: Mombacho, *Oersted* 14829.

COSTA RICA: SAN JOSÉ: vicinity of El General, alt. 640-1100 m., *Skutch* 2250, 2266, 3820, 3852.

It is unfortunate that the type of *H. nodiflorus* (*Heyde & Lux* 4329) has flowers with small apical appendages. The appendages in this species actually are rarely present, and if present are extremely small. This species is characterized by its large leaves, the largest known for the genus, which are nearly glabrous on both the surfaces. The fruit is like that of *H. Donnell-Smithii*, but is more spheroid, slightly more tomentose, and larger in size. It can be distinguished from *H. popayanensis* by its large orbicular fruits, as well as by its glabrous leaves.

INDEX TO EXSICCATAE

Italicized numerals refer to collector's numbers, *s. n.* (*sine numero*) to unnumbered collections; parenthetical numerals refer to the numerals of taxonomic entities conserved in this revision.

Aguilar, I. *81*(6); *97100*(7).
 Allart, A. *273*, *516*(10).
 Allen, P. H. *641*, *1398*, *1519*, *2849*, *2912*(10).
 André, E. *467*, *800*, *K. 924*, *K. 925*(10).
 Arbelaez, E. P. & Cuatrecasas, J. *5798*(10).
 Ariste-Joseph, Bro. A. *370*(10).
 Baker, C. F. *2490*(10).
 Balansa, B. *2295*(10).
 Bang, M. *1455*, *1491*, *2305*(10).
 Barnes, C. R. & Land, W. G. *285*(1).
 Berlandier, J. L. *1064*(1); *971*(2).
 Brandegee, T. S. *s. n.*(3).
 Brenes, A. *655*(7); *6369*(10).
 Botteri, —. *340*, *341*, *882*, *888*, *992*(8).
 Bourgeau, M. *1200*(1); *1574*, *1819*, *1875*, *1974*(8).
 Britton, N. L. & Broadway, W. E. *467*(10).
 Broadway, W. E. *5199*, *6569*, *9200*(10).
 Buchtien, O. *8125*(10).
 Calderón, G. M. *452*(9).
 Cardenas, M. *2839*(10).
 Christopherson, E. D. *117*(10).
 Collins, G. N. & Doyle, C. B. *252*, *255*(7).
 Conzatti, C. *s. n.*, *4313*(1); *1694*(8).
 Cook, O. F. & Griggs, R. F. *204*, *722*(7).
 Cowell, J. F. *270*, *271*(10).
 Cuatrecasas, J. *10925*, *13262*, *13340*(10).
 Cuatrecasas, J., Schultes, R. E. & Smith, E. *12237*, *12471*, *12590*(10).
 Cumming, H. *1131*(10).
 Curran, H. M. *7*(9); *9*, *17*, *700*, *718*(10).
 Daniel, Bro. *1024*(10).
 Dayton, W. A. *3156*(7).
 Degener, O. *10843*(10).
 Dodge, C. W., Hanckel, R. & Thomas, W. S. *6379*(7).
 Edwards, J. B. *465*(11).
 Emrick, G. M. *192*(5).
 Englesing, F. C. *136*, *140*(7).
 Ervendberg, L. C. *225*(9).
 Espiña, —. & Giacometto, —. *20861*(10).
 Fendler, A. *1277*, *1277B*(10).
 Ferris, R. S. *6025*(5).
 Fiebrig, K. *2a*(10).
 Fröderström, H. & Hulten, E. *860*(8); *780*(9).
 Frost, S. W. *218*(10).
 Funck & Schlim *150*(10).
 Galeotti, H. *4154*(6); *4162*, *4162B*(8).
 Garnier, A. *560*(9).
 Gaumer, G. F. *1234*, *1315*, *2275*, *2302*, *23488*, *24177*(6).
 Gentle, P. H. *2273*(6); *1534*, *2297*, *2355*, *2788*, *3203*(9); *1787*, *3204*, *3470*(11).
 Gentry, H. S. *1644*, *1709*, *2440*, *5069*, *6607*(3); *4792*(4).
 Ghiesbreght, M. *51*(6).
 Goldman, E. A. *226*(3); *70*(8); *37*(9).
 Goll, G. P. *255*(9).
 Gonzalez, J. *860*(4).
 Greenman, J. M. *161*(8).
 Haenke, T. *2468*(2).
 Hagen, C. von & Hagen, W. von. *107*(7); *1010*, *1070*, *1224*(11).
 Hahn, L. *1340*(9).
 Halbinger, C. *61*(1).
 Hancock, W. *12*(5).
 Harvey, D. R. *5258*(10).
 Hassler, E. *557*, *557a*, *11856*(10).
 Hauman, —. *9206*(10).
 Hayes, S. *437*, *947*, *1015*(10).
 Heyde, E. T. *381*(6); *637*, *658*(11).
 Heyde, E. T. & Lux, E. *3956*(6); *4177*, *4329*(11).
 Hinton, G. B. *2723*, *4953*, *5119*, *6736*, *7077*, *12449*, *12477*, *13246*, *14831*(1); *2843*, *5109*, *5369*, *5416*, *7036*, *7155*, *7236*, *7243*, *13398*(2); *4265*, *6605*, *6621*, *6724*, *6876*, *6901*, *6905*, *6906*, *9801*, *9802*, *10901*(5).
 Holton, I. F. *770*(10).
 Hunter, A. A. & Allen, P. H. *304*(10).
 Jack, J. G. *8689*(10).
 Jimenez, D. *993*(10).
 Johnston, J. R. *1106*, *1332*(6).
 Jones, M. E. *27153*, *97400*(1).
 Jorgenson, P. *4500*(10).
 Juzepczuk, —. *1461*(1).
 Kellerman, W. A. *6068*, *6448*(9).
 Kerber, E. *276*, *483*(8).
 Killip, E. P. *8248*(10).
 Killip, E. P. & Smith, A. C. *15009*, *15518*, *19481*, *25864*(10).
 Klug, C. *3076*, *3627*, *4395*(10).
 Krukoff, B. A. *5261*, *10249*, *10283*, *10409*(10).
 Langlassé, E. *572*(1); *623*(5).
 Lawrence, A. E. *590*(10).

Leavenworth, W. C. & Hoogstraal, H. 1731, 1525(5).
 Lehmann, F. C. B.T. 553, 5502(10).
 Lemmon, J. G. & Lemmon, —. s.n., 251 (1).
 LeSueur, H. 1404(3); 661, 1158(4).
 Lévy, P. 483(7).
 Liebmann, F. M. 473(1); 522, 523(6); 477(7); 471, 475, 478 (8).
 Linden, J. 858, 898(6); 1609(7); 857 (8).
 Lundell, C. L. 959, 1192(6); 4177, 6516 (11).
 Lundell, C. L. & A. A. Lundell 7821(9).
 Lyonnet, E. 1178(1); 1190, 1726(2).
 MacBrude, J. F. 2713, 4065, 4765(10).
 Martinez, M. s.n., 110(1); 222(8).
 Maxon, W. R. 4751(10).
 Maxon, W. R. & Hay, R. 3156(6); 3305, 3306, 3322(7).
 Medellin, R. 92(8).
 Mell, C. D. 670(9).
 Mexia, Y. 809(1); 1100(2); 7141(10).
 Miguel, H. A. 105(10).
 Morales, J. 1.122(6).
 Muller, C. H. 3634(4).
 Müller, F. 884, 1037, 1049(8).
 Mutis, J. C. 1474, 1478, 3921, 4383(10).
 Narvaez-Montes, M. & Salazar, A. E. 860 (4).
 Nelson, E. W. 1243, 1485, 1818, 3520, 7046(1); 2298, 6970(2); 3400(6); 4383 (7); 70, 119(8).
 Orcutt, C. R. 4463, 4465(5); 3068(8).
 Ortega, J. G. 3087(3); 3130, 4612(4).
 Ostenfeld, C. H. 50(10).
 Palmer, E. 157(2); 97, 100, 191, 620(3); 99, 647, 732, 733(4); 440, 986(5).
 Pennell, F. W. & Killip, E. P. 6337, 8097 (10).
 Piper, C. V. 5532, 5612(10).
 Pittier, H. 13022(6); 273, 2305, 3082, 5392, 11975, 12605, 13022(10).
 Poeppig, E. 1894, 3102, 3627(10).
 Pringle, C. G. 1791, 8227, 8719, 9692, 9693(1); 8694(2); 10069(5); 6106(8).
 Purpus, C. A. 3062(1); 7524(2); 2227, 15704(6); 2226, 2387, 8275(8).
 Record, S. J. & Kuylen, H. H. 25, G. 99 (6); 9958(7); 10034(8).
 Reed, E. 449(10).
 Regnell, A. F. III 285(10).
 Reko, B. P. 4448, 4571(1).
 Renson, C. 61(6).
 Rimbach, A. 288(10).
 Rodriguez, J. V. 1679(6).
 Rojas, S. 534(7).
 Rose, J. N. 2305, 2496, 3090(1); 1694 (3); 2860a, 2860b(5).
 Rose, J. N. & Hough, W. 4335, 4565, 4828(1); 4314(7); 4304(8).
 Rose, J. N. & Painter, J. H. 7390, 7537, 7646(1); 7389(5).
 Rose, J. N. & Rose, G. 23518(10).
 Rose, J. N., Standley, P. C. & Russell, P. G. 12828(4).
 Rovirosa, J. N. 120(9).
 Rowlee, W. W. & Rowlee, H. E. 212(7).
 Rozynski, K. 782(8).
 Ruiz, H. & Pavon, J. 39/8, 39/9(10).
 Rusby, H. H. 1492, 1493(10).
 Saer, J. 778(10).
 Savon, M. 503(1).
 Sawada, M. 101(10).
 Schipp, W. A. S. 589(6); 872(9).
 Schunke, C. 290, 293(10).
 Seler, C. & E. 4196, 4829(1); 5381(2); 3766(8); 4976(9).
 Shattuck, O. 662, 754(10).
 Simmonds, N. W. 281(10).
 Skutch, A. F. 3922, 4226(7); 3346(10); 1445, 1763, 2037, 2250, 2266, 3820, 3852(11).
 Smith, A. H. 1358, Ny. 1263(10).
 Smith, C. L. 1002(9).
 Smith, H. H. 1908(10).
 Smith, J. D. 1723(7); 1722(9).
 Smith, J. G. 284(8); 234(9).
 Smith, L. C. 797, 939(1).
 Sneidern, K. von. 434, 1431(10).
 Solis Rojas, F. 354(7).
 Soukup, J. 790(10).
 Spruce, R. 4558(10).
 Standley, P. C. 19303, 19660, 20304, 50888, 64273, 78068, 80064, 81067(6); 54096(7); 55149, 55154, 55518(9); 31552(10); 53854, 55791, 55793, 56640, 63443, 88541(11).
 Standley, P. C. & Valerio, J. 44633, 45148 (7); 44147(10).
 Stevenson, N. S. 336(9).
 Steyermark, J. A. 30577, 31912, 44076, 52218(6); 44342, 45229, 48987, 49169 (7); 44067, 44068, 45229(9); 52694, 52754, 52878(10); 35467, 43825, 52113 (11).
 Stork, —. 1158(10).
 Sumichrast, —. 882(8).
 Tate, R. 31(384)(7).
 Thieme, C. 5160(10).
 Tonduz, A. 7451, 8453, 14828(6); 8561 (7).

1949]

KO KO LAY—REVISION OF HELIOCARPUS

541

Toro, R. A. 206, 784, 846, 887(10).
 Triana, J. s. n., 5367(10).
 Tuerckheim, H. von 7828, 8500(7).
 Urbina, —. 639(1).
 Velasco, L. V. 8997(6).
 Venturi, S. 1002, 1002c, 7074, 9205(10).
 Vogl, P. C. 50a(10).
 Warming, E. 313(10).
 Weberbauer, A. 3432, 7124(10).
 Werdermann, E. 2126(10).
 Wetmore, R. H. & Abbe, E. C. 108(10).
 White, P. 29(10).
 Williams, L. 8273, 8288, 8289, 8400,
 8526, 8527(7); 4297, 9957, 10692(10).
 Williams, R. O. 649, 650, 12671(10).
 Williams, R. S. 827(10).
 Wilson, C. L. 197, 198(9).
 Woodworth, R. H. & Vestal, P. A. 730,
 748(10).
 Woronow, G. 2333(1); 2963(7); 2947,
 3038(8).

NEW APOCYNACEAE OF SOUTH AMERICA

DAVID DE AZUMBUJA¹
AND ROBERT E. WOODSON, JR.

SECONDATIA Adolphi Azambuja, spec. nov. Frutex altissime scandens lactescens; ramulis crassiusculis glabris in maturitate conspicue lenticellatis. Folia ovato-elliptica vel lanceolata basi rotundata vel obtusa apice anguste acuminata saepe mucronata 5–8 cm. longa 2.0–4.5 cm. lata firme membranacea vel leviter coriacea glabra supra nitidula subtus opaca ibique albida et tenuissime reticulata; petiolis 0.6–0.7 cm. longis. Inflorescentia terminalis laxe cymosa pauciflora folia subtendentia paulo superans; pedicellis 0.7–1.1 cm. longis glabris; bracteis minimis. Calycis laciniæ ovato-triangulares acutæ 2.5–3.0 mm. longæ intus cum squamis parvis longis. Corolla salverformis tubo 6–7 mm. longo in regione staminium insertionis leviter dilatato intus puberulente lobis oblongo-linearibus vel linearilanceolatis obliquis 15–17 mm. longis glabris patentibus. Stamina prope basim tubi corollæ inserta; antheris oblongo-sagittatis 3.5–4.0 mm. longis dorso puberulentis. Ovarium rotundatum 1.2–1.5 mm. altum minute puberulentum; stigmate 1.2 mm. alto subsessili basi dilatato ubique duos annulos superpositos efformatum; disco annulare ovario multo minore. Folliculi fusiformi compressi et prope basim maxime dilatati apicem versus gradatim angustati lignosi striati 19–20 cm. longi ca. 3.5 cm. lati; seminibus oblongo-ellipticis coma e fasciculis pilorum opacorum argentorum reflexorum.—BRAZIL: AMAZONAS: Manaus, matas de terras altas a nordeste de Flores, Sept. 14, 1945, A. Ducke 1,758 (fl.); same locality, Aug. 29, 1947, A. Ducke 2,105 (fr.), in Herb. Jard. Rio de Janeiro no. 60,224.

This species is dedicated to my friend Dr. Adolpho Ducke. Although similar to *S. Duckei* in habit, the flowers of *S. Adolphi* are shorter than those of the latter because of the difference in size of the corolla lobes.

LACMELLEA speciosa Woodson, spec. nov. Arbores. Folia opposita breviter petiolata late oblonga acuta basi obtusa 14–18 cm. longa 5.5–8.0 cm. lata coriacea glabra; petiolis 7–8 mm. longis. Inflorescentia ut videtur terminalis sed versimiliter in axillis foliorum superiorum lateralis; pedunculo 5–7 mm. longo, bracteis ovatis minimis; floribus speciosis albidis subsessilibus. Corollæ salverformis tubum ca. 3 cm. longum, faucibus paulo ampliatis ca. 5 mm. longis; lobis ca. 1.3 cm. longis 4 mm. latis. Calycis laciniæ late subreniformes rotundatae ca. 2 mm. longæ piloso-ciliatae. Antherae lineares 4 mm. longæ. Pistillum 1 cm. longum in ovario gradatim ampliatum; stigmate ca. 2 mm. longo. Fructus ca. 3.5 cm. diam. lutei; seminibus 2.—COLOMBIA: DEL VALLE: Río Calima (region del Choco), La Trojita, 5–50 m. alt., Feb. 19–March 10, 1944, J. Cuatrecasas 10568, in Herb. Missouri Bot. Gard., HOLOTYPE.

¹ Agrônomo Silvicultor, Forest Service, Brazil.

Issued November 30, 1949.

This species is particularly noteworthy because of the corolla lobes which are much longer than those of any other known species of the genus. Since the lobes are nearly thrice the length of the corolla throat, a redefinition of Markgraf's (Notizbl. 15:618-619. 1941) sections *EULACMELLEA* and *ZSCHOKKEA* is required. Less satisfactory would be the erection of a third section to accommodate *L. speciosa*, merely on the basis of corolla proportions.

MALOUETIA parvifolia Woodson, spec. nov. Arbores graciles vel fructices lactescentes ca. 4-5 m. alti; ramulis gracilibus cortice nigris. Folia opposita brevisime petiolata late ovato-elliptica 4.5-5.5 cm. longa 2-3 cm. lata late obtusa basi obtusa vel rotundata subcoriacea glabra subtus cum domatiis parvis; petiolis 0.2-0.3 cm. longa. Inflorescentiae axillares pauciflorae subsessiles. Flores parvi albi; pedicellis cum pedunculo petiolaris subaequantibus. Corollae salverformes tubo cylindrico 5-gono ca. 0.4 cm. longo basi ca. 0.1 cm. diam. extus glabro, lobis oblique lanceolatis acuminatis 0.8-0.9 cm. longis valde patulis intus papillatis. Calycis laciniae valde imbricatae late ovatae scariaceae ca. 0.2 cm. longae cum squamellis internis marginalibus solitariis. Antherae paene inclusae anguste lanceolato-sagittatae ca. 0.3 cm. longae dorso apicem versus sparse pilosulae. Ovaria ca. 0.5 mm. longa puberulo-papillata cum nectariis 5 fere aequilongis; stigmate fusiformi ca. 1 mm. longo cum stylo aequilongo. Folliculi linearis-fusiformi 6-9 cm. longi ca. 0.3 cm. crassi glabri; seminibus 2.5 cm. longis valde canaliculatis sparse pilosis.—VENEZUELA: AMAZONAS: aquático, en las margenes abiertas y completamente inundadas cerca de la boca del Río Sanariapo, arriba de Raudal de Maipures, alt. 120 m., Feb. 7, 1942, L. Williams 15968, in Herb. Missouri Bot. Gard., HOLOTYPE.

This species, like that immediately preceding, was received from the U. S. National Herbarium a few years ago in an exchange of unnamed duplicates. *M. parvifolia* apparently is most closely allied to *M. cestroides*, of the *Robbia*-complex, but differs from it quantitatively in almost every detail.

MALOUETIA grandiflora Woodson, spec. nov. Arbores lactescentes ca. 8 m. altae; trunco ca. 12 cm. diam., ramulis gracilibus cortice tenui fere nigro. Folia opposita subsessilia late elliptica acuminata basi acuta 20-25 cm. longa 7-9 cm. lata glabra subcoriacea subtus sine domatiis. Inflorescentia terminalis umbelliformis pauciflora, pedunculo ca. 0.5 cm. longo, bracteis scariaceis minimis. Flores speciosissimi albi; pedicellis gracillimis ca. 2.5 cm. longis; calycis lacinii aequalibus plus-minus imbricatis ovato-trigonalibus acutis 0.4 cm. longis scariaceis papillatis intus cum squamellis alternatis solitariis bifidis; corolla infundibuliformi extus glabra vel indistincte papillata, tubo proprio valde arcuato ca. 3.5 cm. longo basi ca. 0.3 cm. diam. apicem versus sensim attenuato, faucibus conicis ca. 1.5 cm. longis ostio ca. 1 cm. diam., limbi lobis oblique ovatis late acutis ca. 2 cm. longis basi 1.5 cm. latis paulo patulis; ovariis late oblongoideis ca. 0.2 cm. longis dense puberulo-papillatis cum nectariis 5 compressis ca. 0.7 cm. longis, stylo gracili ca. 1.2 cm. longo, stigmate oblongo-fusiformi ca. 0.2 cm. longi; antheris anguste lanceo-

1949]

AZUMBUJA & WOODSON—NEW APOCYNACEAE

545

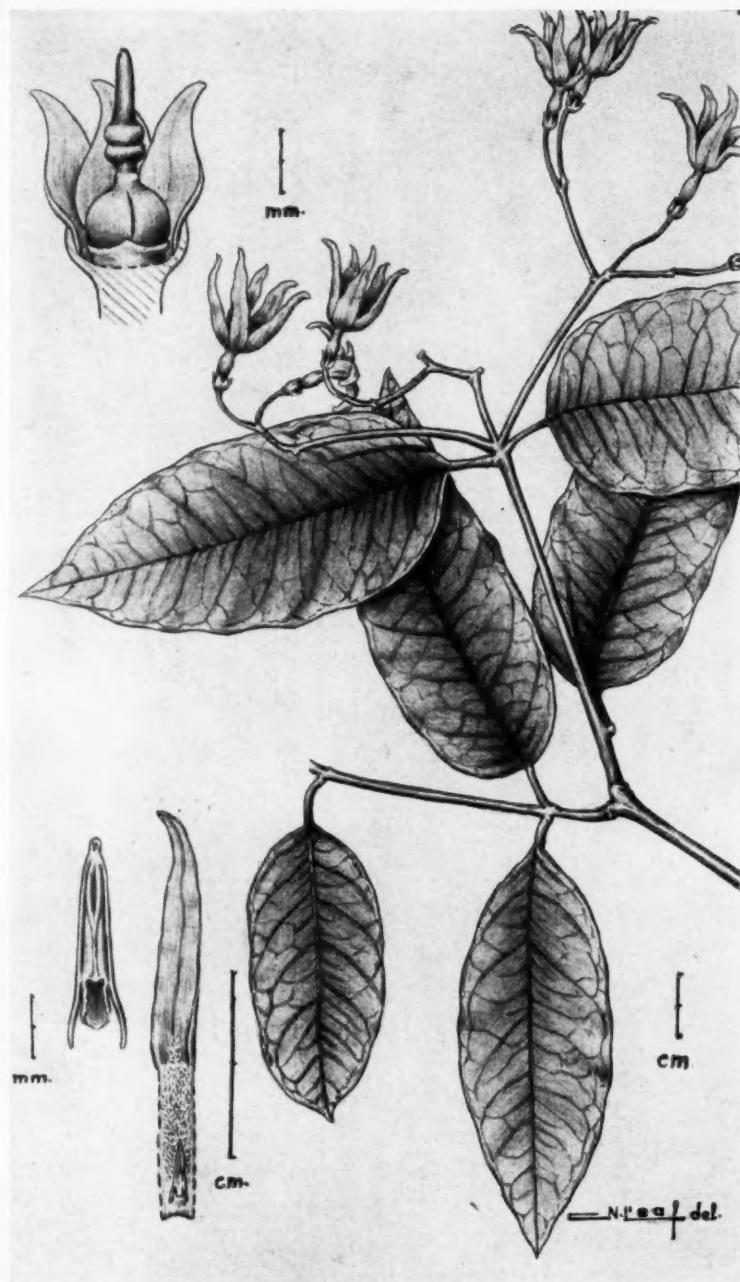
lato-sagittatis paene inclusis ca. 0.6 cm. longis dorso apicem versus sparse pilosulis. Fructus ignoti.—VENEZUELA: AMAZONAS: Maroa, Río Guainía, alt. 127 m., Feb. 10, 1942, L. Williams 14237, in Herb. Missouri Bot. Garden, HOLOTYPE.

For a *Malouetia*, this species is almost alarming, with its relatively gigantic, infundibuliform corollas so alien to its cogners. Surely it will be made the type of a distinct subgenus by the next monographer of the genus. I am persuaded to forbear the erection of a new genus because the affinities of *M. grandiflora* so obviously are with *Malouetia*, as seen in the habit of the plants, the rather distinctive bark, the leaves (although our specimen is without the domatia found with more or less regularity in the other species), and the structure of the inflorescence and reproductive organs.

EXPLANATION OF PLATE

PLATE 40

Habit and floral dissections of *Secondaria Adolphi* Azumba.

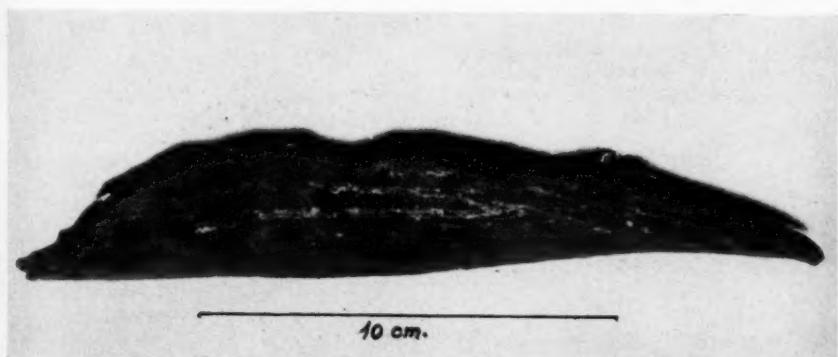
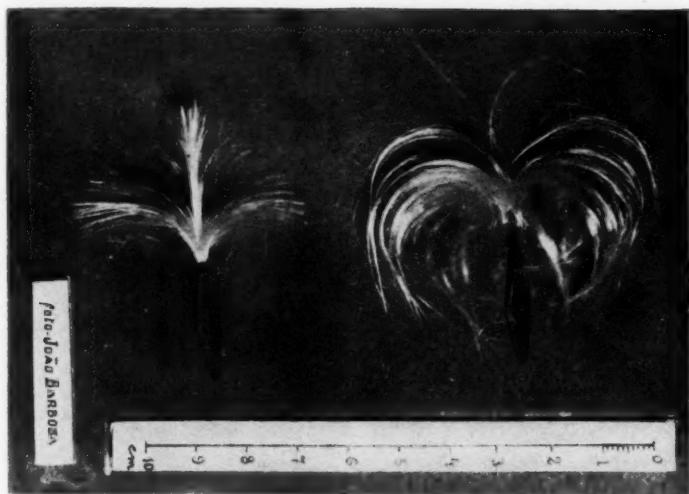


AZUMBUJA & WOODSON—NEW APOCYNACEAE

EXPLANATION OF PLATE

PLATE 41

Fruit and seed of *Secondaria Adolphii* Azumbuja.



AZUMBUJA & WOODSON—NEW APOCYNACEAE

GENERAL INDEX TO VOLUME XXXVI

New scientific names of plants and the final members of new combinations are printed in **bold-face** type; synonyms and page numbers having reference to figures and plates, in *italics*; and all other matter in ordinary type.

A

Adenodiscus, 511; *mexicanus*, 523
 Allen, P. H. Orchidaceae of Panama (third part), 1; (fourth part), 133
 Ancash, On some uses of maize in the Sierra of, 405
 Anderson, Edgar: Charles M. Rick and. On some uses of maize in the Sierra of Ancash, 405; Stoner, C. R., and. Maize among the Hill Peoples of Assam, 355
 Andrews, Henry N., Jr. *Nucellangium*, a new genus of fossil seeds previously assigned to *Lepidocarpon*, 479
 Aneurophyton, 291
 Apocynaceae of South America, New, 543
 Asia: maize in, 389; distribution of major races in, 391
 Assam, Maize among the Hill Peoples of, 355
 Assam hills: economics in the, 375; history in the, 374; map of, 357; tribes of, 356; varieties of maize among the, 359
 Azumbuja, David de, and Robert E. Woodson, Jr. New Apocynaceae of South America, 543

B

Baxter, Robert W. Some Pteridosperm stems and fructifications with particular reference to the Medullosae, 287
 Beer prepared from maize: in Assam, 377, in Peru, 410
 Bhutan, maize in, 372
 Burma, maize in, 373

C

Calamopitys, 291
 California, Assamese varieties of maize grown in, 356, 379
 Callejon de Huilas, uses of maize in the, 406
 Cancha, preparation of, from maize, 409
 Carboniferous plants, 287, 479
 Cardiocarpus, 492; *bicuspidatus*, 493; *injens*, 492; *minor*, 492
 Chicha, preparation of, from maize, 410; *chicha de jora*, 410; *chicha morada*, 411

Chochaca, preparation of, from maize, 411
Chondrorhyncha aromatica, 85; *caloglossa*, 85; *costaricensis*, 86; *discolor*, 87; *marginata*, 88, 89
 Chromosomes in *Paphiopedilum*: comparative length of, in *P. Lawrenceanum* and *P. callosum*, 441, 443; numbers of, 445; terminal, 453, 468
 Coal balls, fossils found in, 287, 479
 Coix, uses of, by the Assamese tribes, 358
Cordiaanthus spicatus, 493
Cusqueño blanco, 406
Cypripedium, 433
Cypripedium, 433; *callosum*, 434; *Hyeanum*, 435; *Lawrenceanum* var. *Hyeanum*, 435
 Cytology: of *Paphiopedilum callosum*, 447; of *P. Maudiae* Hort., 433, 449; of *P. Lawrenceanum*, 448; analysis of root-tips, 440; of yeasts, 260

D

Dafla tribe of Assam, maize culture by the, 368, 398
 Darrah, W. H., description of coal-ball fossil by, 479
Dolerotheca, 315; *formosa*, 316, 344, 348; *Reedana*, 317; *Schopfii*, 317, 348, 350, 352; *selerotica*, 315, 316, 346, 348, 352; *villosa*, 317

E

Economics in the Assam hills, 375
Euspermatopteris, 294
 Ethnology in relation to maize, 355, 405

F

Ferns, fossil, 287
 Food plants among the Hill Peoples of Assam, 374
 Fossil: fructifications, 315; seeds, 479; stems, 287

G

Galactose, fermentation of, 260, 265
Grewia terebinthifolia, 513

H

Heliocarpus, A revision of the genus, 507; generic relationships, 507; economic value of, 509; geographic distribution, 509; taxonomy, 511; vernacular names, 510
Heliocarpus, 511; *americanus*, 528, 532; *americanus* var. *popayanensis*, 532, var. *typica*, 528; *appendiculatus*, 526; *attenuatus*, 520; *australis*, 532; *belizensis*, 523; *boliviensis*, 532; *costaricensis*, 523; *Caecaliae*, 530; *chontalensis*, 526; *cuspidatus*, 530; *climatus*, 532; *Donnell-Smithii*, 530; *excelsior*, 536; *floribundus*, 530; *Gentlei*, 536; *glaber*, 517; *glabrescens*, 523; *glanduliferus*, 523; *horridus*, 530; *laevis*, 521; *mexicanus*, 523; *microcarpus*, 513; *Nelsonii*, 513; *nodiflorus*, 536; *occidentalis*, 521; *pallidus*, 515; *Palmeri*, 517; *polyanthus*, 517, var. *nodiflorus*, 536; *popayanensis*, 532; *popayanensis* var. *grandifolius*, 532, var. *Schumannii*, 532, var. *trichopoda*, 532; *reticulatus*, 513; *Rosei*, 532; *rufus*, 532; *stipulatus*, 532; *subtrilobus*, 532; *terebinthinaceus*, 513; *tomentosus*, 528; *trichopodus*, 532; *velutinus*, 515; *viridis*, 520; *yucatanensis*, 523

Hermann, Frederick J. New species of *Lonchocarpus* from Panama, 281

Heterangium *Griegii*, 204; *Kukuki*, 294; *minimum*, 294

Hybrids: of *Paphiopedilum*, 433; of *Saccharomyces*, 259

I

Inheritance in yeast, 260

Internode diagram of a variety of Assamese maize, 381

Iowa, fossils found in coal-balls from, 287, 479

J

Job's tears, use of, by the Assamese tribes, 358

K

Kaloxylon, 293

L

Lacistema speciosa, 543

Lay, Ko Ko. A revision of the genus *Helicarpus* L., 507

Lepidocarpon, 486; *glabrum*, 479, 491; *lomaxi*, 486

Lonchocarpus, New species of, from Panama, 281

H

Lonchocarpus atropurpureus, 282; *calcaratus*, 282; *densiflorus*, 284; *glabrescens*, 284; *oliganthus*, 281; *parviflorus*, 282; *praecox*, 284
Lyginopteris, 290

M

McQuade, Henry A. Cytology of *Paphiopedilum Maudiae* Hort., 433

Maiz dulce, 409; maiz morada, 411

Maize: among the Hill Peoples of Assam, 355, culture of, 376; geographic distribution of, 405; history of, 405; in hill areas outside Assam, 372; in the Orient, 355; morphological survey of, grown by the Nagas, 379; On some uses of, in the Sierra of Ancash, 405; races of, in South America and Asia, 390; uses of, in Assam, 377, in Peru, 405; varieties of, 380, 383
Maize: "Caribbean", 383; "Drooping Waxy", 381, 386, 402; "Early Slender", 383, 400; "Early Upright", 384, 404; "Late Side-wise", 381, 385, 402; "Late Upright", 383, 384, 404

Malouetia cestroides, 544; *grandiflora*, 544; *parviflora*, 544

Manioc, culture of, in the Assam Hills, 374

Manipur State: maize in, 373; tribes of, 357

Marsilea, 492

Medicine, use of corn preparations in, 409

Medullosa, 290; *anglica*, var. *oiensis*, 298; *centrofilis*, 298; *distelica*, 298; *elongata*, 301; *endocentrica*, 303; *Leuckartii*, 298; *Noei*, 298; *primaeva*, 298; *Thompsonii*, 298

Medullosae, Some Pteridosperm stems and fructifications with particular reference to the, 287

Melibiose, fermentation of, 260, 265

Mendelian, Non-, segregations in *Saccharomyces*, 259

Mierspermatopteris aphyllum, 289, 322, 324; partial reconstruction of, 382

Millet, use of, by the Assamese tribes, 358

Monba tribe of Assam, 358, 396; threshing maize, 396; maize stacked for ripening, 396

Mote, preparation of, from maize, 411

Mundkur, Balaji D. Evidence excluding mutations, polysomy, and polyploidy as possible causes of non-Mendelian inheritance in *Saccharomyces*, 259

N

Naga tribes of Assam, 357, 359, 398; corner of a "jhum" field, 398; varieties of maize

grown by, 379; characteristics of, 384
 Nepal, maize in, 373
 Non-Mendelian segregations in Saccharomyces, Evidence as possible causes of, 259
 Nucellus, fossil, 480, 486
 Nucellangium, a new genus of fossil seeds previously assigned to Lepidocarpon, 479
 Nucellangium glabrum, 491

O

Olla canchera, a prehistoric vessel used to parch maize, 409, 409
 Orient, maize in the, 355
 Orchidaceae: of Panama (third part), 1, (fourth part), 133; Index (part III), 247; Pfitzer's key to Pleonandreae of, 434; Rolfe's key to suborder Diandreae of, 434

P

Paleobotany studies, 287
 Panama: Flora of, Part III, Fascicle 4 (Orchidaceae, third part), 1, Fascicle 5 (Orchidaceae, fourth part), 133; Index to Part III, 247; New species of Lonchocarpus from, 281; A first record of the genus Qualea in, 285
 Paphiopedilum Maudiae Hort., The cytology of, 433
 Paphiopedilum, 433; albino forms of, 437; chromosome numbers in, 445; cytology of *P. callosum*, 447, of *P. Lawrenceanum*, 448, of *P. Maudiae*, 449; key to subgenera, 435; meiosis in, 447; root-tips, 440; taxonomy of, 433
 Paphiopedilum: "Alma Gavaert", 438; bellatulum, var. album, 437; callosum, 434, 437, 441, 447, 466, list of crosses in which used as parent, 459, var. Sanderae, 433, 434, 437, 459; Charlesworthii var. album, 437; Curtisi, 437; "Emerald", 438; "Enchantress", 438; Holdenii, 438; insigne var. Sanderae, 438, var. Sanderianum, 438; Lawrenceanum, 435, 437, 448, 466, list of crosses in which used as parent, 462, var. Hyeanum, 433, 435, 437; Maudiae, 433, 435, analysis of, 448, list of crosses in which used as parent, 456, var. "Bank House", 436, var. "Dell", 436, var. magnificum, 436, 466, var. "Westonbirt", 436; niveum, 437; Rosettii, 438; "Warden", 438
 Paphiopedilum, 433
 Peru, uses of maize in Ancash, Dept. of, 405
 Psilophyton princeps, 295
 Photographing spores of Selaginella, 414
 Pbragmopedium, 433
 Pbragmopedium, 433

Phytolaccaceae, 475
 Pollen grains: of *Paphiopedilum callosum*, 447, 470; of *P. Lawrenceanum*, 449, 470; of *P. Maudiae*, 450, 470
 Polynesians, transfer of crops by, 292
 Popcorns: in Assam, 379; Oriental, 355; in Peru, 409
 Potato, culture of, in the Assam Hills, 374
 Pteridosperm stems and fructifications, Some, with particular reference to the Medullosae, 287

Q

Qualea, A first record for the genus (Vochysiaceae), in North America, 285
 Qualea cymulosa, 285; rupicola, 286

R

Rhetinangium, 290
 Rice in the Assam Hills, 358
 Rick, Charles M., and Edgar Anderson. On some uses of maize in the Sierra of Ancash, 405
 Rogers, David J. Stegnosperma: A new species and a generic commentary, 475

S

Saccharomyces: Evidence excluding mutations, polysomy and polyploidy as possible causes of non-Mendelian inheritance in, 259; tetrad analyses of crosses of, 260
 Schery, Robert W.: A first record for the genus Qualea (Vochysiaceae) from North America (Panama), 285; Robert E. Woodson, Jr., and collaborators. Flora of Panama, Part III, Fasc. 4, 1, Fasc. 5, 133
 Schopfiastrum, 291
 Secondaria Adolphi, 543, 546, 548; Duckei, 543
 Seed-ferns, 288; comparative characters of stem genera of, 290
 Seeds, fossil, 479, "normal", 480, "proliferated", 486
 Segregations in yeast, Non-Mendelian, 259, 271
 Selaginella, Spores of the genus, in North America north of Mexico, 413
 Selaginella, 413; acanthonota, 419, 426; apoda, 423, 431; arenicola, 418, 425; arizonica, 422, 430; armata, 413, 414, 422, 431; asprella, 420, 421, 429; Biegelovii, 417, 418, 425; cinerascens, 419, 427; Ser. Circinatae, 423; Coryi, 418; Ser. Decumbentes, 422; densa, 413, 420, 421, 429; Douglasii, 422, 431; eremophila, 422, 430; subg. Euselaginella, 415, 417

floridana, 419, 426; *funiformis*, 419, 426;
Hansenii, 421, 422, 430; *lepidophylla*, 423,
 431; *leucobryoides*, 420, 428; *mutica*, 419,
 427; *neomexicana*, 418; *oregana*, 419,
 426; *Parishii*, 422; *pilifera*, 413, 423, 431;
Riddellii, 418, 425; *rupestris*, 413, 417,
 420, 421, 429; *rupincola*, 417, 418, 425;
scopulorum, 420, 421, 429; *selaginoides*,
 413, 414, 415, 417, 424; *Sheldoni*, 422,
 430; *Sherwoodii*, 417, 424; *sibirica*, 421,
 428; subg. *Stachygynandrum*, 416, 422;
Standleyi, 420, 428; *tortipila*, 414, 417,
 424; *Underwoodii*, 419, 427; *Wallacei*,
 413, 421, 428; *Watsonii*, 420, 427;
Wrightii, 421, 430

Selenipedium, 433

Selenipedium, 433

Sierra of Ancash, uses of maize in, 406

Sikkim, maize in, 372

Sorghum: relation between maize and, 393;
 use of, by the Assamese tribes, 358

South America, New Apocynaceae of, 543;
 maize of, 389, 405

Sporangium, fossil, 480, 486

Spores of the genus *Selaginella* in North
 America north of Mexico, 413

"Star rings" from carboniferous species of
Medullosa, 312, 338, 340, 342

Stegnosperma: A new species and a generic
 commentary, 475; *cubense*, 476; *balimifolia*,
 477; *halimifolium*, 475, 477; *balimifolium*,
 476; *scandens*, 476; *Watsonii*, 475

Stem genera of seed-ferns, 290

Stems and fructifications, Some PteridospERM, with particular reference to the
Medullosae, 287

Stenomylon, 291

Stonor, C. R., and Edgar Anderson. Maize
 among the Hill Peoples of Assam, 355

Sutcliffia, 291

T

Tercio pelo, 409

Tetrad analyses of yeast hybrids, 260, 268

Tiestos, 409

Tocos, preparation of, from maize, 406

Trichilia scandens, 476

Triumfetta, 1; *mexicana*, 523

Tryon, Alice F. Spores of the genus *Selaginella* in North America north of Mexico, 413

V

Valcárce's illustration of *Olla canchera*, 409

Vitamin synthesizing abilities in yeasts, seg-
 regations of, 271

Vochysiaceae, the genus *Lonchocarpus* of
 the, 285

W

Woodson, Robert E., Jr., and David de
 Azumbuja. New Apocynaceae of South
 America, 543; Robert W. Schery and,
 and collaborators. Flora of Panama, Part
 III, Fasc. 4, 1, Fasc. 5, 133

Y

Yeast hybrids, tetrad analysis of, 260

Yeast, see *Saccharomyces*

Z

Zea Mays—see Maize

, 1949

Maize
55

, 268

96

Selag-
fexico,

ra, 409

ts, seg-

pus of

vid de
South
y and,
a, Part

0